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ON THE CRAYFISH GENUS *FALLICAMBARUS* (DECAPODA: CAMBARIDAE) IN ARKANSAS, WITH NOTES ON THE *FODIENS* COMPLEX AND DESCRIPTIONS OF TWO NEW SPECIES

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Abstract.—The genus *Fallicambarus,* embracing 16 species of burrowing crayfishes, is represented in Arkansas by eight of them, five of which are members of the nominate subgenus and three assigned to the subgenus *Creaserinus.* A key is provided for the identification of the 16, the combined ranges of which extend from Ontario to southwestern Texas and southwestern Georgia, and from South Carolina to Maryland. *Fallicambarus* (*F.*) *petilicarpus,* a close relative of *F.* (*F.*) *dissitus,* is described from Union County, Arkansas, and *F.* (*C.*) *gilpini,* related to *F.* (*C.*) *caesius,* from Jefferson County, Arkansas. Data are presented for placing *Fallicambarus* (*C.*) *uhleri* (Faxon) and *F.* (*C.*) *hedgpethi* (Hobbs) in the synonymy of *F.* (*C.*) *fodiens* (Cottle). For each of the species occurring in Arkansas, as a complete a synonymy as possible is offered along with a diagnosis of the species; also included are a statement of the range, a list of localities (also noted on spot maps) and specimens examined, color notes, size ranges of adults, and life history and ecological notes.

Among the more interesting and least known of the crayfishes of Arkansas are eight species assigned to the genus *Fallicambarus.* Like all of their congeners, those occurring in Arkansas are seldom found in permanent bodies of water, and, as adults, only after rains or during floods do they frequent temporary pools or runoff. Throughout most of their lives, these crayfishes inhabit burrows that are excavated in areas where, for most of the year, the water table does not drop more than a meter or so beneath the surface (in Arkansas, such areas exposed to the sun often may be recognized by the presence of hydrophilic sedges). Turrets, sometimes in the form of slender chimneys, but more often irregular mounds of earthen pellets of a size proportional to that of the crayfish, mark the scattered burrows which, in many areas, may be seen in, or adjacent to, roadside ditches. Less frequently, clusters of mounds, or even entire fields studded with turrets signify the presence of large colonies of these crayfishes.

Although seldom seen during daylight hours, on warm evenings individuals, with chelipeds extended, may be observed at the mouths of their lairs, sometimes perched at the top of a chimney, or, when the humidity is sufficiently high, and particularly following a shower, walking over the ground. During the early spring and after rains, evidence of the presence of a crayfish in its domocile is provided by damp-to-wet pellets of soil recently deposited at openings to the burrows. Such signs of recent excavation are seen most frequently early in the day, before the pellets have become dry, but, if the weather is overcast, recent deposits may be found at almost any hour.

At one time or another, there exist for most burrows constructed by members of the genus *Fallicambarus* more than one opening at the surface that lead into the sim-

ple or complex system of galleries. The simplest burrows constructed by these crayfishes in Arkansas are those of *F.* (*C.*) *fodiens* (Cottle, 1863). Often they consist of a single subvertical tunnel with a slight enlargement at the fundus, but more often they are made more complex by the addition of a side passage leading to or toward the surface, and on rare occasions, when a second adult shares the domicile with an ovigerous female or one bearing young, there may exist a secondary gallery leading downward. Thus in its simplest form, the burrow consists of passages that are subvertical and are disposed in the forms of an "I," "Y" (sometimes inverted), or "X." The more complex patterns usually occur in areas where during much of the year the water table lies very near or almost at the surface. The galleries of these burrows are disposed largely subparallel to the surface, and except for one or two that descend, presumably to the maximum depth to which the water table drops, lie relatively close to the surface. Usually there are at least two exits, one of them nearly always topped by a turret that is sometimes open, but during dry weather may not only be closed but also the passage leading to it is often "back-filled." If the burrow is that of an ovigerous female or one carrying young, all openings to the surface are frequently plugged. During wet seasons, all of the galleries may be water-filled, but at other times water may be found only at the bottom of the one or two deep passages. A few burrows have been excavated in which no standing water was present.

The range of the genus *Fallicambarus* is a discontinuous one in which the larger segment extends from Ontario southward to Arkansas County, Texas, and eastward to the Apalachicola River basin of southwestern Georgia. The more eastern segment encompasses the Coastal Plain and lower Piedmont provinces from New Jersey to South Carolina. In Arkansas, the genus is confined to the Coastal Plain and foothills of the Ozark and Ouachita mountains. There the nominate subgenus, which is not known to occur east of the Ouachita River basin in Arkansas and Louisiana or west of the Brazos Basin in Texas, is restricted to the Ouachita and Red river basins. The much more widespread subgenus *Creaserinus,* however, occurs in all of the major drainage basins in the state, overlapping much of the range of the subgenus *Fallicambarus.*

Of the eight species present in Arkansas, five are members of the nominate subgenus: *Fallicambarus* (*F.*) *dissitus* (Penn, 1955), *F.* (*F.*) *harpi* Hobbs & Robison (1985), *F.* (*F.*) *jeanae* Hobbs (1973), *F.* (*F.*) *petilicarpus,* new species, and *F.* (*F.*) *strawni* (Reimer, 1966); and three are assigned to the subgenus *Creaserinus*: *F.* (*C.*) *caesius* Hobbs (1975), *F.* (*C.*) *fodiens* Cottle (1863), and *F.* (*C.*) *gilpini,* new species. Little is known about any of them except *F.* (*C.*) *fodiens,* and no investigation has involved a comparison of representatives of populations throughout the range of the species. Moreover, considerations of its relationship to *F.* (*C.*) *uhleri* and *F.* (*C.*) *hedgpethi* have been only cursory, the principal reason being a lack of specimens from much of the suspected or assumed ranges of the three species. In many, if not most, of the collections that were available, there were no first form males. The latter problem persists to date, for in less than half of the collections that we have examined is even one such specimen present. As a result we cannot be confident that the one or two males in a collection exhibit secondary sexual characters, the most useful that we have encountered, that are typical of the local population. In defense of the conclusions offered, however, we point out that such features appear to be remarkably uniform in the first form males in most localities represented in our material by two or more such males. This observation has prompted the question as to why so few of these males have been collected.

The following represents primarily an account of our knowledge of the genus *Falli-*

cambarus in Arkansas, although we have attempted to summarize all available data on those species that range beyond the state boundaries. Indeed, the diversity noted in the populations of *F.* (*F.*) *fodiens* occurring in Arkansas provoked us into a study of representatives of the species throughout its range, one of the largest of any crayfish in North America. In presenting the synonymies, diagnoses, bibliographic references, and summaries of published biological data for each of the species occurring in the state, we have included all of which we are aware, and the following key encompasses all of the species that have been assigned to the genus.

Abbreviations used herein are as follows: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; cl, carapace length; CM, Carnegie Museum, Pittsburgh; pol, postorbital carapace length; TU, Tulane University, New Orleans; USNM, National Museum of Natural History, Smithsonian Institution.

Genus *Fallicambarus* Hobbs (1969a)

Diagnosis.—"Adults with rostrum devoid of marginal spines. Mesial margin of palm of chela with row of fewer than 12 tubercles, opposable margin of dactyl usually with prominent excision. Areola linear or obliterated [along part of its length]. Antennal scale more than twice as long as broad. First pleopods of first form male symmetrical and terminating in two or three distinct parts (mesial process, central projection and, occasionally, cephalic process; caudal element always absent) bent caudally or caudomesially at angle of 90 degrees or more to main shaft or forming broad arc; central projection corneous, blade-like or tapering (but flattened laterally) and [frequently] lacking . . . subapical notch; non-corneous mesial process never bulbiform but often appearing twisted and usually with eminence on cephalic (morphological) border slightly distal to base; cephalic process, when present, small, at least partially corneous, situated mesially at base of mesial process, and directed caudally or caudodistally" (slightly modified from Hobbs 1973:463). Type species: *Cambarus strawni* Reimer, 1966:11. Gender: masculine.

This taxon was proposed by Hobbs (1969a:111) to receive an assemblage of eight species that had been assigned formerly to the genus *Cambarus.* Subsequently, the diagnosis of this assemblage was revised by him (1973:462), and speculations were offered on the interrelationships of the 11 members recognized at the time. In pointing out more formally the existence of two species groups among these crayfishes, he proposed the adoption of two subgenera: the nominate subgenus comprising five species, and the subgenus *Creaserinus,* six. In this summary the former subgenus is considered to consist of seven species, two of which have been described since 1973 and one herein; *F.* (*F.*) *spectrum* has been relegated to the synonymy of *F.* (*F.*) *jeanae* (Hobbs 1989). The subgenus *Creaserinus* as presently constituted consists of nine species, four of which were described since 1973 and one is added in this study. Evidence for placing *Fallicambarus* (*C.*) *hedgpethi* and *F.* (*C.*) *uhleri* in synonymy with *F.* (*C.*) *fodiens* is detailed herein.

Key to Species of Genus *Fallicambarus* (Based on First Form Males)

1.	First pleopod with proximomesial spur (Fig. 3*i*) . . . . (Subgenus *Fallicambarus*) .	2
1′.	First pleopod lacking proximomesial spur (Fig. 11*h*) . . . . . (Subgenus *Creaserinus*) . .	8
2.	Mesial ramus of uropod with distinct distolateral spine (Fig. 1*c*); abdomen not conspicuously narrower than thorax .	3
2′.	Mesial ramus of uropod lacking distinct distolateral spine	

(Fig. 1*d*); abdomen conspicuously narrower than thorax . 5

3. Mesial ramus of uropod with distomedian spine projecting beyond margin of ramus (Fig. 1*c*); cheliped with sufflamen (Fig. 10*z*); central projection disposed proximocaudally, never overlapping that of corresponding pleopod (Fig. 11*h*) ..... *macneesei*

3′. Mesial ramus of uropod with distomedian spine never projecting beyond margin of ramus (Fig. 11*d*); cheliped without sufflamen (Fig. 10*a*′); central projection disposed proximomesially, its distal extremity frequently overlapping that of corresponding pleopod (Fig. 3*i*) 4

4(3′). First pleopod with cephalic process (Fig. 3*b*); length of carpus of cheliped distinctly greater than width of palm of chela (Fig. 3*h*) ..... *petilicarpus*

4′. First pleopod lacking cephalic process (Fig. 1*e*); length of carpus of cheliped subequal to or less than width of palm of chela ..... *dissitus*

5(2′). First pleopod without cephalic process (Fig. 1*f*) ..... *jeanae*

5′. First pleopod with cephalic process (like Fig. 1*g*) 6

6(5′). Ischia of third and fourth pereiopods with hooks (like Fig. 3*n*) ..... *devastator*

6′. Ischia of third pereiopods only with hooks (like Fig. 11*m*) .. 7

7(6′). Cephalic process of first pleopod extending caudodistally (Fig. 1*g*); mesial ramus of uropod without distomedian spine (like Fig. 1*d*) ..... *harpi*

7′. Cephalic process of first pleopod closely paralleling basal part of mesial process (Fig. 10*y*), apical part if free directed caudally; mesial ramus of uropod with distomedian premarginal spine ..... *strawni*

8(1′). Ventral surface of merus of cheliped with one row of tubercles (Fig. 1*q*) 9

8′. Ventral surface of merus of cheliped with two rows of tubercles (Fig. 1*p*) 10

9(8). Mesial surface of dactyl of chela with tubercles in basal half (Fig. 1*r*); mesial ramus of uropod lacking distolateral spine ..... *caesius*

9′. Mesial surface of dactyl of chela lacking tubercles (Fig. 11*o*); mesial ramus of uropod with distolateral spine (Fig. 11*d*) ..... *gilpini*

10(8′). Mesial surface of palm of chela of second pereiopod not bearded (Fig. 1*a*); shaft of first pleopod strongly reflexed (Fig. 1*h, j*) 11

10′. Mesial surface of palm of chela of second pereiopod bearded (Fig. 1*b*); shaft of first pleopod straight or only slightly curved (Figs. 1*i, k, l,* 8, 9, 10*a–x* 13

11(10). First pleopod with central projection not conspicuously long and slender (Fig. 1*h*) *byersi*

11′. First pleopod with central projection conspicuously long and slender (Fig. 1*j*) 12

12(11′). Antennal scale tapering distally to strong distolateral spine (Fig. 1*n*); boss on coxa of fourth pereiopod ridgelike (Fig. 10*c*′) ..... *gordoni*

12′. Antennal scale rounded to subtruncate distally, lacking distolateral spine (Fig. 1*m*); boss on coxa of fourth pereiopod bulbiform (10*b*′) ..... *burrisi*

13(10′). First pleopod with central projection straight and truncate distally (Fig. 1*i*) .... *hortoni*

13′. First pleopod with central projection arched, and tapering at distal extremity or bearing subapical notch (Figs. 1*k*, *l*, 8, 9, 10*a–x* 14

14(13′). Antennal scale with somewhat distinct distal and mesial margins, their junction subangular (Fig. 1*o*); abdomen broadly joined to cephalothorax ..... *fodiens*

14′. Antennal scale with distomesial margin strongly inclined abdomen narrowly joined to thorax 15

15(14′). First pleopod with mesial process conspicuously overreaching central projection (Fig. 1*k*) ..... *danielae*

15′. First pleopod with mesial process overreaching central projection little if any (Fig. 1*l*) ..... *oryktes*

Subgenus *Fallicambarus* Hobbs (1973)

Diagnosis.—First pleopod of male with proximomesial spur and sometimes with cephalic process. Cheliped without sufflamen, except in *F. macneesei,* chela with tubercles scattered over most of dorsal surface, lateral margin of palm and basal part of fixed finger rounded, more often subserrate or serrate, never smoothly costate. Second pereiopod of male with mesial face of chela and carpus lacking dense mats of plumose setae. Coxa of fourth pereiopod usually with conspicuously large boss.

Fallicambarus (*Fallicambarus*) *dissitus* (Penn)
Figs. 1*e*, 2

Cambarus dissitus (Penn, 1955:73–80, figs. 1–13 [Types: holotype, allotype, and morphotype, USNM 98125, 98126, 98127; paratypes, ANSP, AMNH, CM, TU, USNM. Type locality: three miles east of Choudrant, Lincoln Parish, Louisiana.]; 1959:5, 6, 9, 11, 15, 16, 17, figs. 25, 48, 66, 79.—Penn & Marlow, 1959: 202.—Hobbs, 1959:896; 1962:274; 1967: 13.—Black, 1967:173, 178.—Fitzpatrick & Payne, 1968:14.—Hobbs III, 1969:19, 21, tab. 2.

Fallicambarus dissitus.—Hobbs, 1969a:111, 124, 173, fig. 20d; 1972:15, 99, figs. 81c, 82d; 1974b:23, 102, fig. 88.—Feinberg, 1971:26.—Hart & Hart, 1974:26, 30.—Bouchard, 1978:432; 1980:432.—Bouchard & Robison, 1981:26, 29.

Fallicambarus (*Fallicambarus*) *dissitus.*—Hobbs, 1973:463, 477–479, fig. 4.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983:167.—Hobbs & Robison, 1985: 1035.

Diagnosis.—Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus less than, or subsequal to, width of palm of chela. Chela with lateral margin at least weakly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles along at least proximal fourth. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur, lacking cephalic process; central projection strongly arched, inclined laterally at base, its distal part directed proximomesially and often crossing that of corresponding pleopod. Hooks on ischia of third and fourth pereiopods. Boss on coxa of fourth pereiopod moderately strong and compressed. Mesial ramus of uropod with distolateral and distomedian spine, latter premarginal. Telson divided and with spine/s flanking anterolateral flank of suture.

Range and specimens examined.—This crayfish is known from only a few localities in the Red and Ouachita river basins of southern Arkansas (Columbia County) and

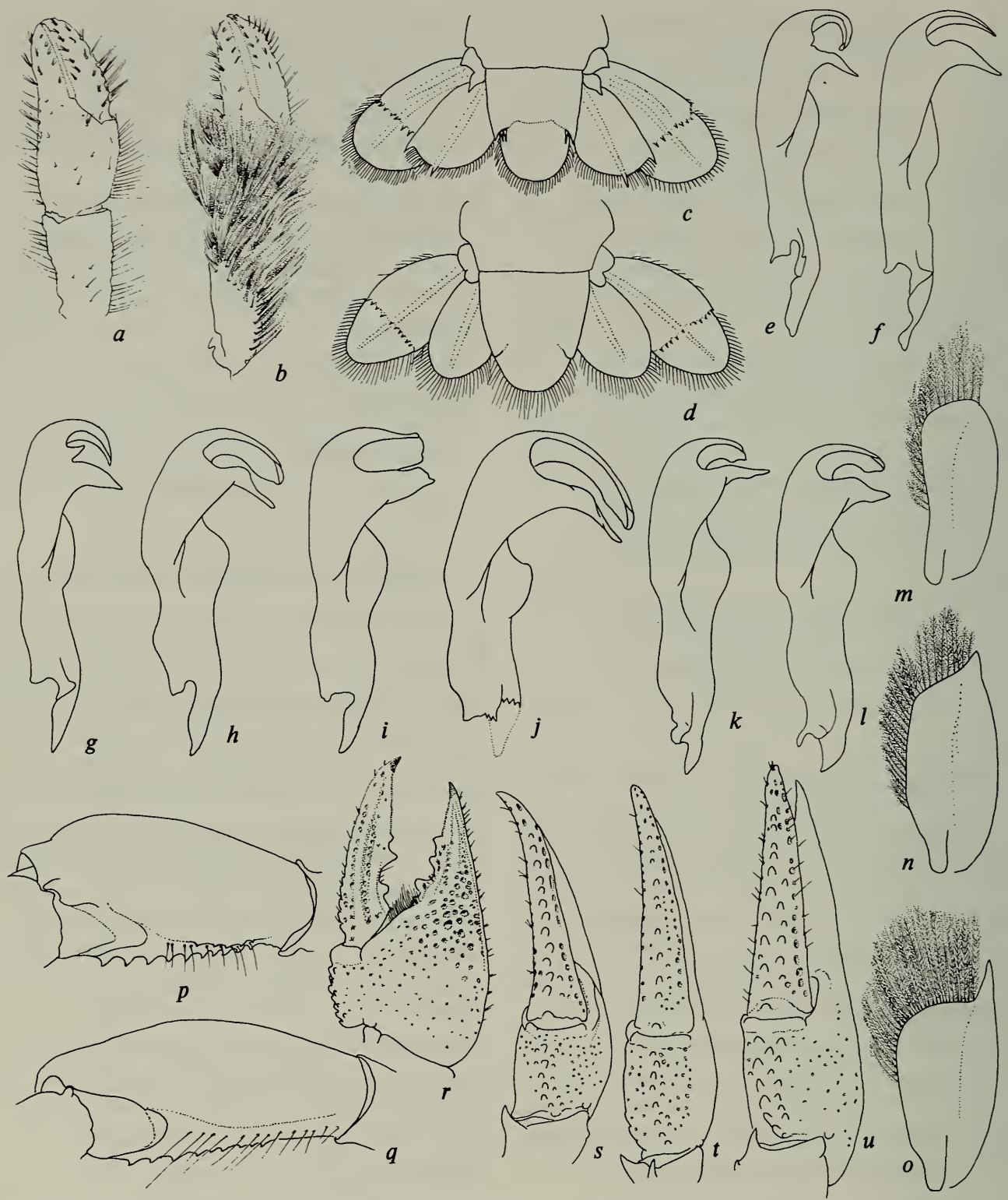

Fig. 1. Characters used in key: a, Distal podomeres of second pereiopod of *Fallicambarus* (*C.*) *byersi*; b, Same of *F.* (*C.*) *fodiens*; c, Dorsal view of telson and uropods of *F.* (*F.*) *macneesei*; d, Same from *F.* (*C.*) *jeanae*; e–l, Mesial view of first left pleopod; e, *F.* (*F.*) *dissitus*; f, *F.* (*F.*) *jeanae*; g, *F.* (*F.*) *harpi*; h, *F.* (*C.*) *byersi*; i, *F.* (*C.*) *hortoni*; *j, F.* (*C.*) *burrisi;* k, *F.* (*C.*) *danielae*; l, *F.* (*C.*) *oryktes*; m–o, Antennal scale: m, *F.* (*C.*) *burrisi*; n, *F.* (*C.*) *gordoni*; o, *F.* (*C.*) *fodiens*; p, Ventrolateral view of merus of cheliped of *F.* (*C.*) *byersi*; q, Same, *F.* (*C.*) *gilpini*; r, Dorsal view of chela of *F.* (*C.*) *caesius*; s–u, Mesial view of chela of *F.* (*C.*) *fodiens*; s, from Ohio; t, from Maryland; u, from Florida.

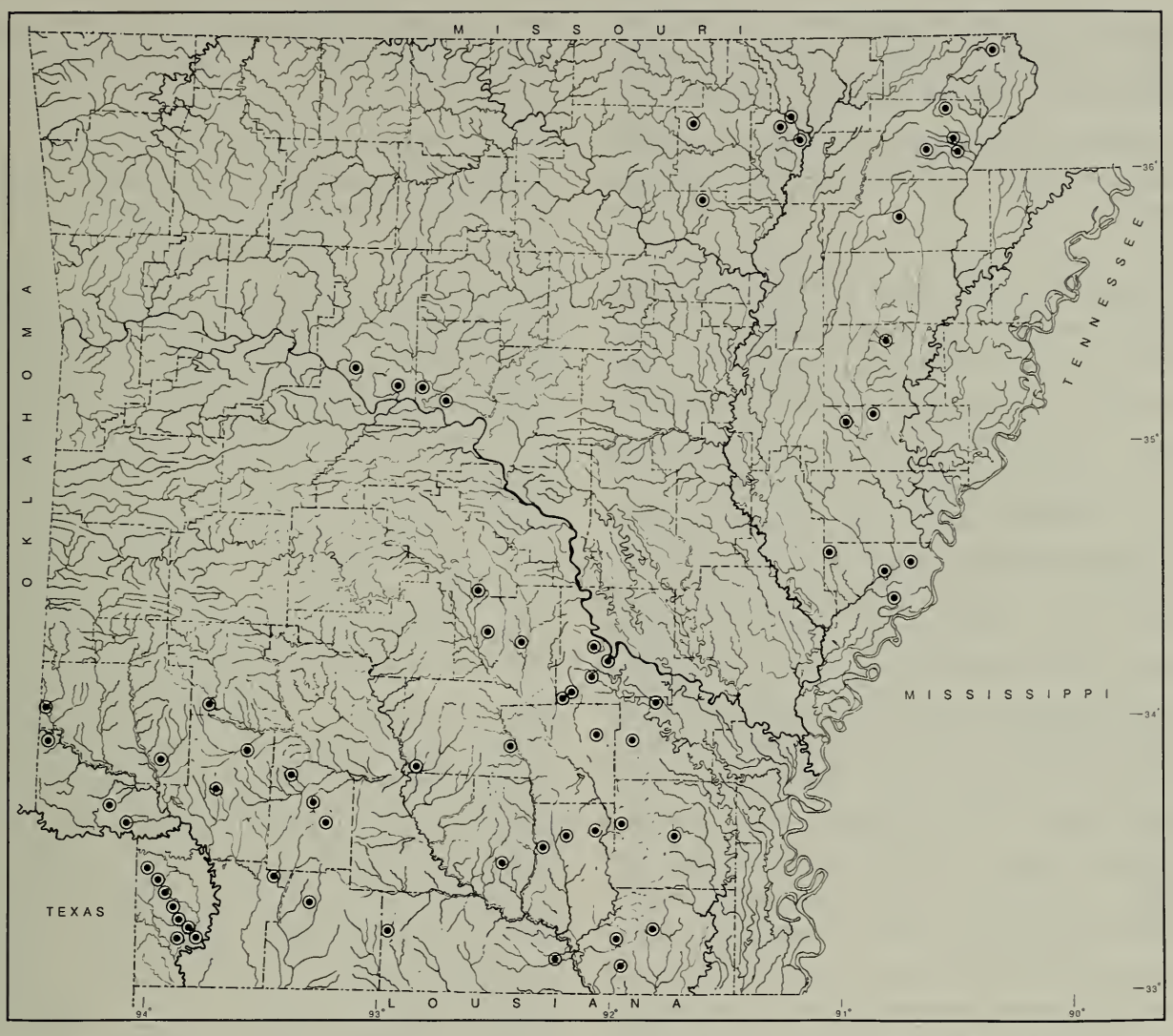

Fig. 2. Distribution of *Fallicambarus* (*F.*) *dissitus* (encircled stars), *F.* (*F.*) *jeanae* (encircled dots), *F.* (*F.*) *petilicarpus* (triangle) and *F.* (*F.*) *strawni* (dots) in Arkansas. (Some localities listed in text too close to others to be shown.)

north central Louisiana (Caldwell, Grant, and Lincoln parishes). It has been found in the following localities in Arkansas. Columbia County: (1) Southern Arkansas University Campus at Magnolia, 1 ♂ I, 23 Apr 1985, HWR. (2) 1 mi SW of Macedonia on St Rte 160, specimens not available, R. W. Bouchard and HWR. These localities lie in the Dorcheat Bayou-Red River basin.

Size.—The largest specimen that we have examined is a first form male from Lincoln Parish, Louisiana, having a cl of 32.7 (pol 29.1) mm. Corresponding lengths of the smallest first form males are 23.1 (20.2) mm.

Life history notes.—First form males have been collected in February, March, April, and May. Neither ovigerous females nor ones carrying young have been reported.

Ecological notes.—Specimens were collected in Grant Parish, Louisiana (8.2 miles, 13.2 km, south of the Winn Parish line on U.S. Highway 167), from moderately complex burrows, approximately two feet deep, in a roadside seepage area; this locality is in a rolling terrain where the soil is a sandy clay. The specimen from locality 1 was collected as it crawled across a lawn where there were chimneys 18 to 24 centimeters in height.

Fallicambarus (*Fallicambarus*) *harpi* Hobbs & Robison

Figs. 1*g*, 5

Fallicambarus (*Fallicambarus*) *harpi* Hobbs & Robison, 1985:1035–1041, fig. 1

[Types: holotype, allotype, and morphotype, USNM 217946, 217947, 217948; paratypes, MHNP, RMHL, USNM. Type locality: see page area 0.2 mi (0.32 km) east of Glenwood, Pike County, Arkansas].

Diagnosis.—Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus less than, or subequal to, width of palm of chela. Chela with lateral margin strongly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles extending almost complete length of finger. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur and freely-projecting (not adnate to mesial process), caudodistally-directed cephalic process; central projection strongly arched, but not inclined laterally at base, and never crossing that of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod very strong and compressed. Mesial ramus of uropod lacking spines. Telson divided but lacking spines.

Inasmuch as no information has been added to our knowledge of this crayfish since it was described, the following data have been extracted from Hobbs & Robison (1985).

Range and specimens examined.—The two nearby localities in the Ouachita River basin cited here are the only ones known for the species. Pike County: (1) Type locality, 36 ♂ I, 13 ♂ II, 8 ♀, 1 j♂, 16 Apr 1982, K. Dillard; 2 ♂ I, 4 ♀, 21 Apr 1982, KD. (2) 0.3 mi (0.5 km) E of Glenwood on US Hwy 70, 6 ♂ I, 3 ♀, 18 Mar 1982, KD.

Color notes.—"Dorsum of cephalic region of carapace, including rostrum very dark, almost black, that of thoracic region greenish tan except for small black triangular spot in open anterior section of areola, narrow band bordering cervical groove, and another band adjacent to posterior margin of carapace; hepatic and mandibular adductor regions also black; orbital, antennal, mandibular, and branchiostegal regions greenish tan. Abdomen with broad median longitudinal, dark red stripe extending from second through fifth segment, becoming pale and disappearing before reaching caudal margin of sixth; lateral part of latter segment, telson, and uropods greenish tan with dark markings; mesial ramus of uropods with black median longitudinal rib. Dorsal surface of cheliped dark green with black suffusion becoming intense mesially so that dorsodistal border of merus, mesial part of carpus, tubercular area of palm, all of dorsum except tips of fingers and proximomesial part of fixed finger almost black; tips of fingers and lateral and ventral surfaces of entire cheliped pinkish to yellowish cream. Remaining pereiopods cream with greenish suffusion marking dorsal parts of podomeres from ischium through propodus, more intense on merus and propodus. Sternal elements and ventral surfaces of pereiopods cream to pinkish cream" (Hobbs & Robison 1985:1039).

Size.—"The largest specimen examined is a female having a carapace length of 39.6 (postorbital carapace length 35.8) mm. The smallest and largest first form males have corresponding lengths of 29.0 (25.8) mm, and 35.4 (31.5) mm, respectively" (Hobbs & Robison 1985:1039–1040).

Life history notes.—First form males were obtained in March and April. Ovigerous females or ones carrying young have not been observed.

Ecological notes.—The type locality consists of a seep "located in a pasture . . . specimens were collected in the early evening as they crawled about in the wet grassy areas. Soil consisted of a sandy clay with some

organic material. Grasses and sedges were abundant. . . ."

Fallicambarus (*Fallicambarus*) *jeanae*
Hobbs
Figs. 1*d, f,* 2

Fallicambarus (*Fallicambarus*) *jeanae* Hobbs, 1973:463–469, 477, 478, 480, figs. 1, 4 [Types: holotype and allotype, USNM 144672, 144673 (♂ I, ♀); paratypes USNM. Type locality: seepage area 1.8 mi (2.9 km) E of Clark County line, Hot Spring County, Arkansas, on St Rte 84.].—Bouchard, 1978:451; 1980:451.—Bouchard & Robison, 1981:28.—Flitzpatrick, 1983: 167, 168.—Hobbs & Robison, 1985:1035, 1040.—Hobbs, 1989.

Fallicambarus (*Fallicambarus*) *spectrum* Hobbs, 1973:463, 469–478, 480, figs. 2, 4 [Types: holotype and allotype, USNM 144674, 144675 (♂ I, ♀); paratypes USNM. Type locality: 2 mi (3.2 km) E of Daisy, Pike County, Arkansas, on US Hwy 70.].—Bouchard, 1978:451; 1980:451.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983:167, 168.—Hobbs & Robison, 1985:1035.

Fallicambarus jeanae.—Hobbs, 1976:550, fig. 1b, d, l.—Bouchard & Robison, 1981: 26.—Huner & Barr, 1981:50, fig 24b, d, l; 1984:45, fig. 24b, d, l.—Robison & Smith, 1982:53

Fallicambarus sp.—Hobbs, 1979:804.

Fallicambarus spectrum.—Bouchard & Robison, 1981:26.—Robison & Smith, 1982:53

Diagnosis.—Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus less than, or subequal to, width of chela. Chela with lateral margin strongly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles extending almost complete length of finger. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur, lacking cephalic process; central projection moderately arched, not inclined laterally at base, its distal part disposed caudoproximally, never crossing that of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod very strong and compressed. Mesial ramus of uropod lacking distolateral spine; distomedian spine, if present, situated premarginally. Telson incised laterally but lacking spines

Range and specimens examined;—This crayfish, which seems to be endemic to the upper Ouachita River basin in southwestern Arkansas, has been found in the following localities (those for which no first form males are listed should be confirmed). Clark County: (1) 1 mi (1.6 km) NE of Amity Center on St Rte 84, Sec 27NE, T5S, R23W, 2 ♂ I, 4 ♀, 1 j♂, 2 j♀, 21 Apr 1973, G. B. Hobbs, J. E. Pugh, HHH; 1 ♂ II, 2 ♀, 2 j♂, 2 j♀, 29 Apr 1976, M. Kearney, HHH; 1 ♂ II, 1 ♀, 1 j♀, 14 Apr 1979, D. D. Koym, HWR; 1 ♂ II, 3 ♀, 3 j♂, 15 Apr 1982, HWR, DDK. (2) roadside ditch 7.4 mi (11.8 km) E of Amity Center on St Rte 84, 1 ♂ I, 1 ♀, 3 j♂, 30 Apr 1976, MK, HHH. (3) Richland Cemetery, 3 mi (4.8 km) NW of Gum Springs, 1 j♂, 1 j♀, 24 Feb 1980, W. Laird. (4) Rest Haven Cemetery 4 mi (6.4 km) W of Arkadelphia on St Rte 8, 1 ♀, 1 j♂, 1 j♀, 24 Sep 1977, E. Laird; 1 j♂, 27 Dec 1979, EL; 3 ♀, 6 May 1980, EL; 2 ♀, 1 j♂, 1 j♀, 12 Feb 1981; 2 ♂ II, 4 ♀, 6 j♂, 5 j♀, 9 Mar 1981, EL, HWR; 1 ♀, 19 Mar 1981, EL. Hempstead County: (5) Blevins, Sec 24, T9S, R24W, 3 ♀, 1 j♂, 29 Apr 1983, P. Lee. (6) Blevins, Sec 6, T10S, R24W, 1 j♂, 1 j♀, 10 May 1983, B. Hill. (7) Blevins, Sec 35, T9S, R25W, 1 ♀, 16 May 1983, T. Chambers. Hot Spring County: (8) roadside ditch 1.8

mi (2.9 km) E of Clark Co line on St Rte 84 (Type locality), 5 ♂ I, 2 ♀, 3 j♂, 2 j♀, 21 Apr 1973, GBH, JEP, HHH. (9) roadside ditch 3.7 mi (5.9 km) E of jct of St Rtes 7 and 84 on latter, 2 ♂ I, 1 j♀, 30 Apr 1976, MK, HHH. (10) roadside ditch 5.2 mi (8.3 km) E of Clark Co line on St Rte 84, 1 j♀, 30 Apr 1976, MK, HHH. (11) roadside ditch 4.5 mi (7.2 km) W of Marcus, 3 ♂ I, 1 ♂ II, 2 ♀, 2 j♂, 5 j♀, 14 Apr 1979, HWR et al. (12) 2.1 mi (3.3 km) E of Point Cedar, 2 ♀, 1 j♂, 1 j♀, 13 Mar 1981, HWR; 1 ♂ I, 2 ♀, 3 j♂, 15 Apr 1982, HWR, DDK. Pike County: (13) roadside ditch 2 mi (3.2 km) E of Daisy on US Hwy 70, 1 ♂ I, 1 ♀, 21 Apr 1973, GBH, JEP, HHH. (14) roadside ditch 2.8 mi (4.5 km) W of Amity Center on St Rte 84, 2 ♂ II, 3 ♀, 2 j♂, 14 Apr 1979, HWR et al. (15) roadside ditch 8.2 mi (13.1 km) W of Amity Center on St Rte 84, 1 j♀, 14 Apr 1979, HWR et al.

Remarks.—With the acquisition of considerably more material than was available to him when *Fallicambarus* (*F.*) *spectrum* was described, Hobbs (1989) concluded that except by the color pattern this crayfish cannot be distinguished from *F.* (*F.*) *jeanae.* The pattern of the former, which is described below, has been observed only in specimens from the type locality. He therefore treated *spectrum* as a color morph of *F.* (*F.*) *jeanae.*

Color notes.—*Fallicambarus* (*F.*) *jeanae* exhibits two distinctive color morphs; that occurring in specimens from the type locality was described by Hobbs (1973:468) as follows: "Dominant color of carapace pale mauve; rostral margins, postorbital ridges, and paired subtriangular areas caudal to postorbital ridges dark brown; latter joining along cervical groove and in caudal gastric area where almost black; caudal margin of carapace dark brown. First abdominal tergum dark brown, remaining ones pale yellowish tan with paired dorsolateral cream splotches and each edged caudally with vermilion. Telson and uropods cream with pale tan suffusion basally. Antennule and antenna with dark yellowish-brown peduncles; flagella with each article yellowish tan basally and dark brown distally; lateral margin of antennal scale almost black. Cheliped mostly yellowish tan dorsally with dark bluish-brown tubercles and bluish-brown suffusion on dorsal margin of merus, dorsomesial surface of carpus, and dorsomesial part of dactyl. Ventral surface of cheliped yellowish cream. Remaining pereiopods with coloration similar to that of cheliped but lacking dark brown tubercles."

The color of the morph that was described under the name of *Fallicambarus* (*F.*) *spectrum* (Hobbs, 1973:472–473) was recorded as follows: "Dominant color of carapace pale mauve gray; rostral margins and postorbital ridges almost black; paired subtriangular reddish-brown markings extending caudally from caudal extremity of postorbital ridges, their basal portions coalescing in median posterior gastric region, slightly overlapping cervical groove, and filling cephalic triangular vestige of areola. Hepatic region with pale reddish-tan suffusion; caudal margin of carapace edged with black. [Dorsolateral parts of branchiostegites provided with conspicuous dark bluish purple (some almost black) spots.] First abdominal tergum reddish brown with succeeding terga progressively fading to uniformly reddish-tan telson and uropods; tergum also fading laterally, and pleuron concolorous with telson. Peduncle of antennule and antenna dark mauve gray, flagella with each article pale tan proximally, becoming dark gray distally; antennal scale with lateral thickened portion almost black. Chelipeds grayish blue dorsally with dark blue tubercles; ventral surface cream; remaining pereiopods similar to cheliped but lacking dark blue tubercles."

Size.—The largest specimen examined by us is a female from Clark County having a cl of 40.6 (pol, 35.5) mm. The smallest and largest first form males have corresponding lengths of 30.0 (26.4) mm and 35.7 (31.7) mm, respectively.

Life history notes.—All of the first form males that we have examined were collected

in April. Neither ovigerous females nor ones carrying young have been observed. A first form male and female were found occupying a single burrow at locality 1 on 21 Apr 1973.

Ecological notes.—The largest colony of this crayfish that we have observed was in the type locality. Persistent rains for at least several days while one of us (HHH) was in the area had brought the water table throughout the seep to the surface, and the mounds marking the entrances to the crayfish burrows were considerably eroded. They did not appear to have been neatly constructed, and the pellets of which subsequently observed turrets were constructed by *F. (F.) jeanae* seemed to have been rather haphazardly affixed to the rim, many having rolled down the side of the crude, vaguely cone like structures. The soil was primarily a sandy clay with gravel and pockets of organic material. The burrows were rather shallow (most of the horizontal passages coursed at depths of 10 to 30 cm; the one or two deeper passages no doubt penetrated the soil for 70 cm to one meter), highly branching, and had two or three openings to the surface. In the immediate vicinity, grasses and sedges were growing in the waterlogged soil, and nearby were trees belonging to the genera *Acer, Juniperus,* and *Pinus.* In April of 1973, the soil was so lacking in firmness that no tool was needed to aid the hand in searching for the crayfish in their burrows. In localities 1 and 13, where the "*spectrum* color morph" was found, the soil was better drained (a small, clear brook flowed through locality 1), the burrows were deeper (but extended no more than a meter beneath the surface), and the horizontal galleries were restricted to a smaller surface area.

Fallicambarus (Fallicambarus) petilicarpus, new species
Figs. 2, 3, 4a

Diagnosis.—Eyes small but pigmented and with faceted cornea. Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus greater than width of palm of chela. Chela with lateral margin weakly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl lacking pronounced excision in basal half, mesial margin with row of tubercles along at least proximal third. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur, and free, caudally projecting cephalic process; central projection strongly arched, inclined laterally at base but projecting mesially and crossing that of corresponding pleopod distally. Hooks on ischia of third and fourth pereiopods. Boss on coxa of fourth pereiopod moderately strong and compressed. Mesial ramus of uropod with distolateral spine, distomedian spine, if present, situated premarginally. Telson divided and with spine/s on anterolateral flank of suture.

Holotypic male, form I.—Body suboval, weakly compressed laterally (Figs. 3*a, l,* 4*a*). Abdomen distinctly narrower than thorax (9.6 and 14.5 mm). Greatest width of carapace near midlength of areola where subequal to height (14.5 and 14.2 mm). Areola linear over most of length and comprising 37.4 percent of entire length of carapace (42.9 percent of postorbital carapace length). Rostrum with convergent, slender margins contracting anteriorly, setting off base of indistinctly delimited acumen, apex of which corneous, upturned, and slightly overreaching midlength of penultimate podomere of antennular peduncle. Dorsal surface of rostrum strongly concave, with submarginal rows of setiferous punctations and scattered ones between. Subrostral ridges rather weak but evident in dorsal aspect to base of acumen. Postorbital ridges also weak but somewhat swollen posteriorly. Branchiostegal and cervical spines absent. Suborbital angle absent. Carapace punctate dorsally and very weakly and sparsely tuberculate laterally;

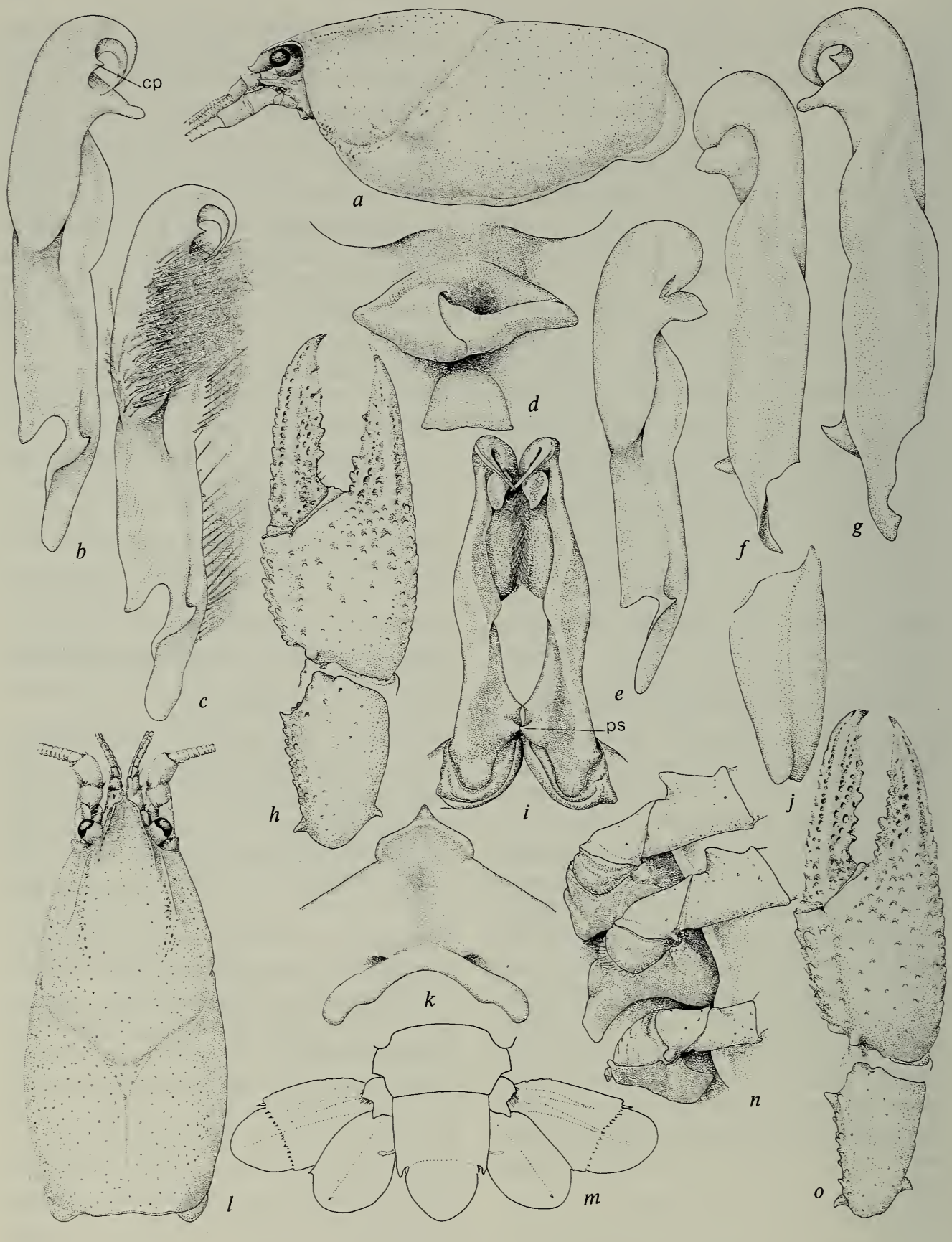

Fig. 3. *Fallicambarus* (*F.*) *petilicarpus* holotype except d, h, j from allotype, and e, f from morphotype): a, Lateral view of carapace; b, c, e, Mesial view of first pleopod, cp cephalic process; d, Annulus ventralis and associated sclerites; f, g, Lateral view of first pleopod; h, o, Distal podomeres of cheliped; i, Caudal view of first pleopods; j, Antennal scale; k, Epistome; l, Dorsal view of carapace; m, Dorsal view of caudal part of abdomen; n, Basal podomeres of third, fourth, and fifth pereiopods. (cp, cephalic process; ps, proximomesial spur.)

extreme anteroventral branchiostegal region inflated, with irregular group of tubercles, seven or eight forming row on ventral flank of cervical groove; fewer tubercles present on dorsal flank of groove.

Abdomen (Fig. 4*a*) little shorter than carapace (28.0 and 30.5 mm); pleura moderately deep and broadly rounded ventrally, only sixth with angular caudoventral margin; pleuron of first abdominal segment clearly overlapped by that of second. Telson (Fig. 3*m*) distinctly divided, and caudolateral angles of anterior section with two pairs of spines, more mesial pair movable. Proximal podomere of uropod with both lobes bearing distal spine, spine on more mesial lobe much stronger than that on lateral lobe; mesial ramus with well developed distolateral spine and smaller premarginal distomedian spine.

Cephalomedian lobe of epistome (Fig. 3*k*) broadly subtriangular with well defined cephalomedian prominence extending cephalodorsally; cephalolateral margins rather smooth; main body of epistome with cephalomedian area depressed but lacking distinct fovea. Ventral surface of proximal podomere of antennule with median spine slightly distal to midlength. Antennal peduncle without spines except on lateral surface of basis at proximal base of antennal scale, flagellum reaching second abdominal tergum. Both antennal scales of holotype with distal extremities missing, but distinctly reduced: blade little broader than thickened lateral portion and apex probably reaching only slightly beyond midlength of penultimate podomere of antennule (see Fig. 3*j, l*). Mandible essentially like that of *Fallicambarus* (*F.*) *devastator* Hobbs & Whiteman (1987: fig. 1i). Ventral surface of ischium of third maxilliped with lateral row of short, plumose setae, and mesial half studded with clusters of long, stiff setae.

Right chela (Fig. 3*o*) approximately 2.4 times as long as broad, not strongly depressed; width of palm slightly more than 1.2 times length of mesial margin, latter bearing row of 7 tubercles subtended dorsolaterally by row of six (left with 6 and 7, respectively); dorsal surface of palm and basal part of fingers studded with squamous tubercles; those along lateral margin forming subserrate row extending from near proximal extremity to about midlength of fixed finger; ventral surfaces of palm, basal third of fixed finger, and mesial part of proximal fourth of dactyl tuberculate; more distoventral part of fingers with punctations, in part, flanking weak median ridges; prominent spiniform tubercle present on oblique distoventral ridge of palm; ventrolateral surface lacking curved row of long setae. Opposable margin of fixed finger with row of 7 tubercles (fourth from base largest) in proximal three-fifths and another (corresponding to usually more ventrally-placed tubercle on the chelae of most cambarids) at base of distal third; minute denticles present between distal 4 tubercles, and, except at base of distalmost tubercle, continuing to corneous tip of finger. Opposable margin of dactyl with row of 5 tubercles (third from base largest; this tubercle marking end of sharp proximal excavation in dactyl of other members of *Fallicambarus*) in proximal three-fourths; mesial margin of dactyl with tubercles forming subserrate row. Dorsal surface of both fingers with well defined median longitudinal ridge.

Carpus of cheliped conspicuously slender and long, almost 1.6 times as long as broad, and longer than either width or mesial margin of palm of chela. Dorsal surface sparsely punctate and bearing poorly delimited and very shallow, oblique, longitudinal furrow; mesial surface with only one prominent subspiniform tubercle, cluster proximoventral to it consisting of much smaller ones; except for ventrodistal extremity bearing usual 2 moderately large tubercles, ventral and lateral surfaces punctate. Merus with single, dorsal, slightly curved row of tubercles, increasing in size distally; lateral surface punctate, and mesial one with polished and granular areas; ventral surface with both mesial and lateral rows of 15 tubercles joined by oblique row of 3. Mesioventral margin of basioischial podomere with only 2 tubercles corresponding to row in other cray-

fishes; compound podomere otherwise with scattered punctations. Chela of second pereiopod with marginal row of setae on palm, and carpus with dorsal row of long setae; mesial surface of carpus and propodus lacking tufts of plumose setae.

Ischia of third and fourth pereiopods (Fig. 3*n*) with simple hooks, neither of which overreaching basioischial articulation and neither opposed by tubercle on corresponding basis. Coxa of fourth pereiopod with prominent, compressed caudomesial boss disposed somewhat in longitudinal axis of body; mesial and lateral surfaces of boss with setiferous punctations. Coxa of fifth pereiopod with small tuberculiform boss extending ventrally from caudomesial angle of podomere; ventral membrane setiferous.

First pleopods (Fig. 3*b, c, g, i*) reaching coxae of third pereiopods, carried deeply in sternum, and largely concealed by setae extending from ventral margin of sternum and from coxae of third and fourth pereiopods. Proximomesial spur well developed. Shaft of appendage only slightly inclined caudally; plumose setae arising from mesial surface of shaft forming feathery plume hiding all or part of each of three terminal elements: mesial process, most proximal of three, non-corneous, somewhat tapering but with rounded apical region, disposed at slightly more than right angle to shaft of appendage; cephalic process smallest, corneous, subtriangular, situated between cephalic process and central projection, and directed caudally; and central projection most conspicuous of three, consisting of long, tapering, bladelike structure reflexed through arc of at least 150 degrees.

Allotypic female.—Differing from holotype other than in secondary sexual characteristics as follows: acumen even less distinctly delimited basally; subrostral ridges evident in dorsal aspect for no more than one-fifth distance from caudal margin of orbit to base of acumen; rudiment of branchiostegal spine present; about same number of tubercles (7 or 8) on both dorsal and ventral flanks of anteroventral segment of cervical groove; spine on lateral lobe of proximal podomere of uropod rudimentary; spine on basis of antenna tuberculiform; flagellum of antenna extending caudally over no more than three-fourths length of areola; chela (Fig. 3*h*) proportionally shorter and broader; mesial row of tubercles on palm of chela subtended dorsally by row of only 5 tubercles; opposable margin of fixed finger with row of 5 tubercles, third from base largest; opposable margin of dactyl with row of 4 tubercles, second from base largest; ventral surface of merus of cheliped with mesial and lateral rows of 14 tubercles; mesioventral margin of basioischial podomere with 3 tubercles (left chela regenerated).

Annulus ventralis (Fig. 3*d*) firmly fused to sternum cephalically, approximately twice as broad as long, and strongly asymmetrical. Cephalic and cephalomedian areas depressed, latter distinctly excavate; dextral side of excavation elevated in massive prominence along mesial margin of which C-shaped sinus marking junction of prominent transverse ridge and prominence; no clearly defined sulcus evident, and fossa hidden. Postannular sclerite about 1.7 times as broad as long and less than half as wide as annulus; lateral margins weakly converging toward broadly rounded anterior extremity; caudal margin irregularly transverse. First pleopods present but not reaching anterior to postannular sclerite.

Morphotypic male, form II.—Differing from holotype as follows: Apex of rostrum reaching base of ultimate podomere of antennule; right branchiostegal spine represented by very small tubercle; proximal podomere of uropod lacking spine on both lobes; antennal peduncle lacking spine on basis, flagellum reaching first abdominal tergum; (as in holotype, distolateral part of both antennal scales broken); chela approximately 2.2 times as long as broad; left chela with only 6 tubercles in mesialmost row on palm; merus of left cheliped with lateral row of only 12 tubercles; mesioventral margin of basioischial podomere with row of 3 or

4 tubercles; hooks on ischia of third and fourth pereiopods and boss on coxa of latter all clearly defined but weaker than those in holotype.

First pleopods (Fig. 3*e, f*) reaching coxae of third pereiopods, symmetrical, and with well defined proximomesial spur; markedly similar in form to pleopod of first form male, but lacking cephalic process, and base of central projection not nearly so distinctly delimited from mesial process.

Color notes.—Basic coloration olive-brown to tan. Carapace dark olive-brown; rostrum and posterior gastric area very dark; lateral areas slightly paler. First abdominal tergum dark olive-brown, second through fifth paler olive-tan and with narrow pinkish tan arc on posteromedian margins; sixth tergum, telson, and uropods dark olive. Antennules and antennae with peduncles olive on brown; flagella reddish brown. Chelipeds with basal three podomeres and proximal part of merus pinkish cream, latter suffused dorsally and laterally with olive, becoming dark olive distally; dorsal tubercles on merus green with white tips. Dorsal and lateral surfaces of carpus bright olive to forest green on brown, tubercles green and largest ones tipped with cream. Chela olive-brown dorsally; distal ridge on palm suffused with green, and green on dorsal flank of opposable borders of both fingers; palm and fixed finger fading ventrolaterally to pinkish orange, ventral surface of all podomeres of cheliped pinkish to lavender cream. Remaining pereiopods with olive suffusing distal part of merus, carpus, and, except that of second pereiopod, proximal part of merus, otherwise pale pinkish cream.

Size.—The largest specimen examined is a female having a cl of 31.8 (pol 27.6) mm. The smaller of the two known first form males, the holotype, has corresponding lengths of 30.5 and 26.6 mm, respectively. Neither ovigerous females nor ones carrying young are available for determining measurements.

Type locality.—Roadside seepage 0.2 mile east of the Columbia County line on State Route 57, Union County, Arkansas (T16S, R18W, Sec 21). A field of young planted trees (*Pinus*) was adjacent to the seep and ditch which supported a moderate growth of sedges and grasses. Specimens were collected from relatively shallow, but complex burrows which, constructed in a sandy loam and topped by chimneys from 8 to 10 cm high, descended to depths of approximately 0.5 m. Some of them penetrated tangled, dense root mats of grasses growing in and on the banks of the ditch. No other crayfish was found in the immediate area.

Disposition of types.—The holotype, allotype, and morphotype (USNM 219507, 219508, and 219509, respectively) are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes consisting of 1 ♂ I, 1 ♂ II, 3♀, and 9 juveniles.

Range and specimens examined.—All of the specimens available were collected at the type locality by the second author on 30 Apr 1982 (1 ♂ I, 1 ♂ II, 2 ♀, and 3 juv) and 28 Mar 1988 (1 ♂ I, 2 ♂ II, 2 ♀, 6 juv).

Variations.—Among the adult specimens, the areola constitutes from 35.2 to 38.5 percent of the total length of the carapace, and from 39.8 to 43.6 percent of the postorbital carapace length. In one small male with a carapace length of 21.5 mm, the corresponding ratios are 34.0 and 39.0 percent, respectively. Most of the variations noted fall within the range of those noted in the descriptions of the primary types. The greatest range of differences, barring regenerated appendages, occurs in the numbers of tubercles on the chelipeds: the opposable margin of the fixed finger may have from 4 to 8 tubercles and that of the dactyl 4 to 7; the ventromesial row on the merus ranges from 14 to 16 and the mesiolateral, from 12 to 15. In the female the annulus ventralis occurs in mirrored images of that in the allotype, and the cephalic margin may or may not be firmly fused to the sternum immediately anterior to it. All of the females have a linear series of 3 to 5 long setae closely associated with the distal part of the ven-

Table 1.—Measurements (mm) of *Fallicambarus* (*F.*) *petilicarpus*.

	Holotype	Allotype	Morpho-type
Carapace:			
Entire length	30.5	29.5	29.5
Postorbital length	26.6	25.8	26.6
Width	14.5	13.9	13.0
Length	14.2	13.3	12.6
Areola:			
Width	0	0	0
Length	11.4	11.1	10.2
Rostrum:			
Width	4.4	4.2	4.6
Length	5.1	4.5	4.8
Right chela:			
Length, palm mesial margin	9.3	4.6	7.3
Palm width	10.9	8.0	8.9
Length, lateral margin	24.5	16.1	19.4
Dactyl length	14.6	10.5	11.2
Abdomen:			
Width	9.6	10.1	9.0
Length	28.0	27.3	26.0

trolateral row of tubercles on the merus; such seem not to be present in the available males. (See Table. 1 for other morphometric differences.)

Life history notes.—The only collections of this crayfish available are two lots collected at the type locality in March and April. A first form male was obtained in both samples. Ovigerous females and ones carrying young have not been observed.

Ecological notes.—See "Type locality."

Relationships.—*Fallicambarus* (*F.*) *petilicarpus* is more closely allied to *F.* (*F.*) *dissitus* than to any other member of the genus. The unusual first pleopods of the males of the two species with caudomesially disposed, crossing (at least sometimes) central projections, are so nearly alike that only after a detailed re-examination of specimens of the former was the distinctive feature, the presence of a small, but well-defined cephalic process, observed. Subsequent comparisons of the two revealed, among the many similarities, two other readily observed features that set *F.* (*F.*) *petilicarpus* apart: the very long slender carpus of the first cheliped and the unique absence in *Fallicambarus* of a distinct concavity on the opposable margin at the base of the dactyl of the chela. The absence of this concavity, a feature the presence of which has served in keys until now to distinguish members of the genus *Fallicambarus* from *Cambarus*, necessitated the slight modifications in the generic diagnosis included herein.

Etymology.—The name describes the slender carpus of the cheliped: *Petilus* (L. = slender) + *carpus* (L. = wrist).

Fallicambarus (*Fallicambarus*) *strawni* (Reimer)

Figs. 2, 10*y*

Cambarus strawni Reimer, 1966:9, 11–14, figs. 9–18 [Types: holotype, allotype, and morphotype, USNM 116675, 116676, 116677 (♂ I, ♀, ♂ II); paratypes, R. D. Reimer. Type locality: small marshy area in the Saline River basin, 2.7 mi (4.3 km) north of Dierks, Howard Co., Arkansas.].—Hobbs, 1967:12; 1968:K16, fig. 32; 1969a:111.—Black, 1967:173, 178.—Bouchard, 1972:61.—Hobbs III et al., 1976:24.

Fallicambarus strawni.—Hobbs, 1969a:103, 111, 124, 151, 173, figs. 2f, 13j, 20i; 1972: 99, 147, fig. 81b; 1974b:24, 100, fig. 81; 1976:551, fig. 1b, e.—Bouchard & Robison, 1981:26.—Robison & Smith, 1982: 53.

Fallicambarus (Fallicambarus) strawni.—Hobbs, 1973:461–479, figs. 3c, h, 4.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983:168.—Hobbs & Robison, 1985:1035.

Diagnosis.—Cheliped without sufflamen; ventral surface of merus with mesial and lateral rows of tubercles; length of carpus less than, or subequal to, width of palm of

chela. Chela with lateral margin strongly serrate, dorsal surface with scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles extending almost complete length of finger. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod with proximomesial spur, and cephalic process adnate to mesial process, if free distally, then directed caudally, parallel to mesial process; central projection comparatively weakly arched, not inclined laterally at base, and disposed caudally, never crossing that of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod very strong and compressed. Mesial ramus of uropod lacking distolateral spine, distomedian spine, if present, situated premarginally. Telson entire, lacking spines.

Range and specimens examined.—This crayfish seems to be endemic to southwestern Arkansas (although there is every reason to believe that it will be found in eastern Oklahoma) where it has been collected only in the Little and Saline watersheds in the Red River basin and in the Little Missouri watershed in the Ouachita River basin. We have examined all of the following material except that collected in locality 6. Howard County: (1) Type locality, 1 ♂ I, 1 ♂ II, 1 ♀, 22 Jun 1963, R. D. Reimer; 2 ♂ I, 1 ♂ II, 1 ♀, 1 j♂, 1 j♀, 21 Apr 1973, GBH, JEP, & HHH; 1 ♀, date ?, R. W. Bouchard. (2) roadside ditch 5.1 mi (8.2 km) W of Athens on St Rte 84, 1 ♂ I, 1 ♀, 29 Apr 1976, MK & HHH. (3) seep 1.8 mi (2.9 km) E of Polk Co line on St Rte 4, 3 ♀, 3 ♂ II (one ♂ later molted to form I), 29 Apr 1976, MK & HHH. (4) roadside ditch 1.8 mi (2.9 km) E of Sevier Co line on US Hwy 70, 3 j♂, 6 j♀, 10 Apr 1982, HWR. (5) Nashville, 1 ♂ II, 10 Apr 1986, L. Morris. (6) Reimer (1966: 4) cited this crayfish from 4 mi W of Umpire on St Rte 4. Pike County: (7) roadside ditch 1.3 mi (2.1 km) E of Little Missouri River on St Rte 84, 1 ♀, 1 j♂, 29 Apr 1976, MK, HHH. (8) roadside ditch 0.9 mi (1.4 km) NE of Howard Co line on US Hwy 70, 1 ♂ I, 1 ♀, 21 Apr 1973, GBH, JEP, HHH. Sevier County: (9) seep and ditch 0.1 mi (16 km) NE of jct of US Hwys 71-59 and 70 on latter, 4 ♂ I, 4 ♂ II, 13 ♀, 2 j♂, 5 j♀, 20 Apr 1973, GBH, JEP, HHH. (10) seep 8.3 mi (13.3 km) E of jct of US Hwys 59-71 and 70 on latter, 1 j♀, 28 Apr 1976, MK, HHH. (11) seep 0.2 mi (0.32 km) E of jct of US hwys 71 and 59 on latter, 1 j♂, 1 ♀, 26 Apr 1976, RWB. (12) 5.8 mi (9.3 km) E of jct on St Rtes 41 and 24 on latter, 1 j♂, 9 Apr 1982, HWR. (13) seep 5.0 mi (8.0 km) NE of jct of US Hwys 59-71 and 70, 1 ♂ I, 20 Apr 1973, GBH, JEP, HHH.

Color notes.—(Based primarily on first form male from locality 8.) Dominant color of carapace pinkish cream to purplish tan overlain by various shades of gray and vermilion. Most of dorsum of cephalic region pinkish tan fading laterally to buff, often with lavender suffusion; rostrum and postorbital ridges very dark gray margined in almost black; caudal gastric area and cervical groove pale to dark gray; cephalic triangle of areola dark gray to almost black, and linear part and caudal triangle of areola vermilion; paired pale gray longitudinal stripes flanking linear areola; remainder of branchiostegites, excluding dark bluish gray caudal margin, very pale cream tan. Tergum of first abdominal segment and cephalic part of that of second dark bluish red, otherwise yellowish tan with vermilion splotches dorsally, fading caudally, and all pleura lighter tan ventrally. Telson largely translucent but with vermilion to brick red splotches cephalically, laterally, and along caudal margin; uropod similarly translucent, but peduncle reddish tan, lateral ramus with reddish splotches lateral to median rib and over entire distal section, and mesial ramus with red pigment largely restricted to median rib and distal third. Chelipeds basically

tan but with dense reticulations of slate blue on dorsum of distal half of merus, that of carpus, and most of that of chela; lateral surface of palm pinkish cream. Exposed parts of peduncles of antennule and antenna mostly gray, and flagella with each article buff proximally, becoming dark gray distally. Lateral margin of antennal scale very dark gray. Remaining pereiopods similar to cheliped, although with more red and less blue pigment on fifth. Ventral surface of body and pereiopods cream, latter with blue pigment toward distal ends of merus and carpus.

In first form male from locality 2 (Howard County), dorsal cephalic region darker orange tan, and with dark brownish-gray area extending across posteromedian gastric region abutting cervical groove; thoracic region more apricot-colored dorsally, fading to cream tan ventrally; anterior triangle of areola almost black, branchiocardiac suture vermilion to scarlet, and posterior triangular area dark reddish brown. Abdomen much darker than carapace, terga of first two segments almost black anteriorly fading rapidly to brick red caudally; succeeding segments with paired subrectangular reddish black splotches (gradually narrowing on posterior segments) dorsolaterally, flanking median glossy brick red longitudinal stripe, red spreading laterally on posterior part of each segment and spilling ventrally onto dorsal part of pleura, which mostly pale pinkish cream with posterior maroon spot. Telson, uropods, and chelae as described above.

Size.—The largest specimen available is a female from Sevier County (locality 9, above) having a cl of 37.2 (pol 32.4) mm. The smallest and largest first form males have corresponding lengths of 24.8 (22.2) mm and 31.9 (28.5) mm, respectively.

Life history notes.—First form males have been collected in April and June. Neither ovigerous females nor ones carrying young have been observed.

Ecological notes.—This crayfish, like *F.* (*F.*) *jeanae,* constructs highly branching (complex) burrows in sandy clay soil. The largest colony visited by us was found at locality 9. There the roadbed is somewhat elevated above the adjoining wooded area (chiefly *Pinus*), and on the northern shoulder of the elevated area, there is a seep in which scores of turrets mark the burrows of this crayfish. When one of us (HHH) first visited this locality in April 1973, the sandy clay soil was water-logged, and one could easily open and follow the complex system of galleries with one's bare hands. On a visit three years later, following a period without rain, there were few turrets in the hard, dry ground, and, even with the aid of a shovel and considerable effort, only one juvenile was found!

Subgenus *Creaserinus* Hobbs (1973)

First pleopod never with proximomesial spur or cephalic process. Cheliped with sufflamen; chela with tubercles on mesial surface of palm but sparse or lacking dorsolaterally and laterally, lateral margin costate. Second pereiopod of male with mesial face of chela and carpus often bearing dense mats of plumose setae (lacking in *F.* (*C.*) *burrisi, F.* (*C.*) *byersi, F.* (*C.*) *caesius, F.* (*C.*) *gilpini,* and *F.* (*C.*) *gordoni*). Type species: *Astacus fodiens* Cottle, 1863:217. Gender: masculine.

Fallicambarus (*Creaserinus*) *caesius* Hobbs

Figs. 1*r,* 5

Fallicambarus (*Creaserinus*) *caesius* Hobbs, 1975:24–28, 33, fig. 7 [Types: holotype, allotype, and morphotype, USNM 144921, 133922, 133923 (♂ I, ♀, ♂ II); paratypes, USNM. Type locality: Roadside ditch at Hot Spring-Saline county line, Arkansas, on St Rte 67.]; 1981:269.—Bouchard, 1978:451; 1980:451.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983:168; 1987:439.

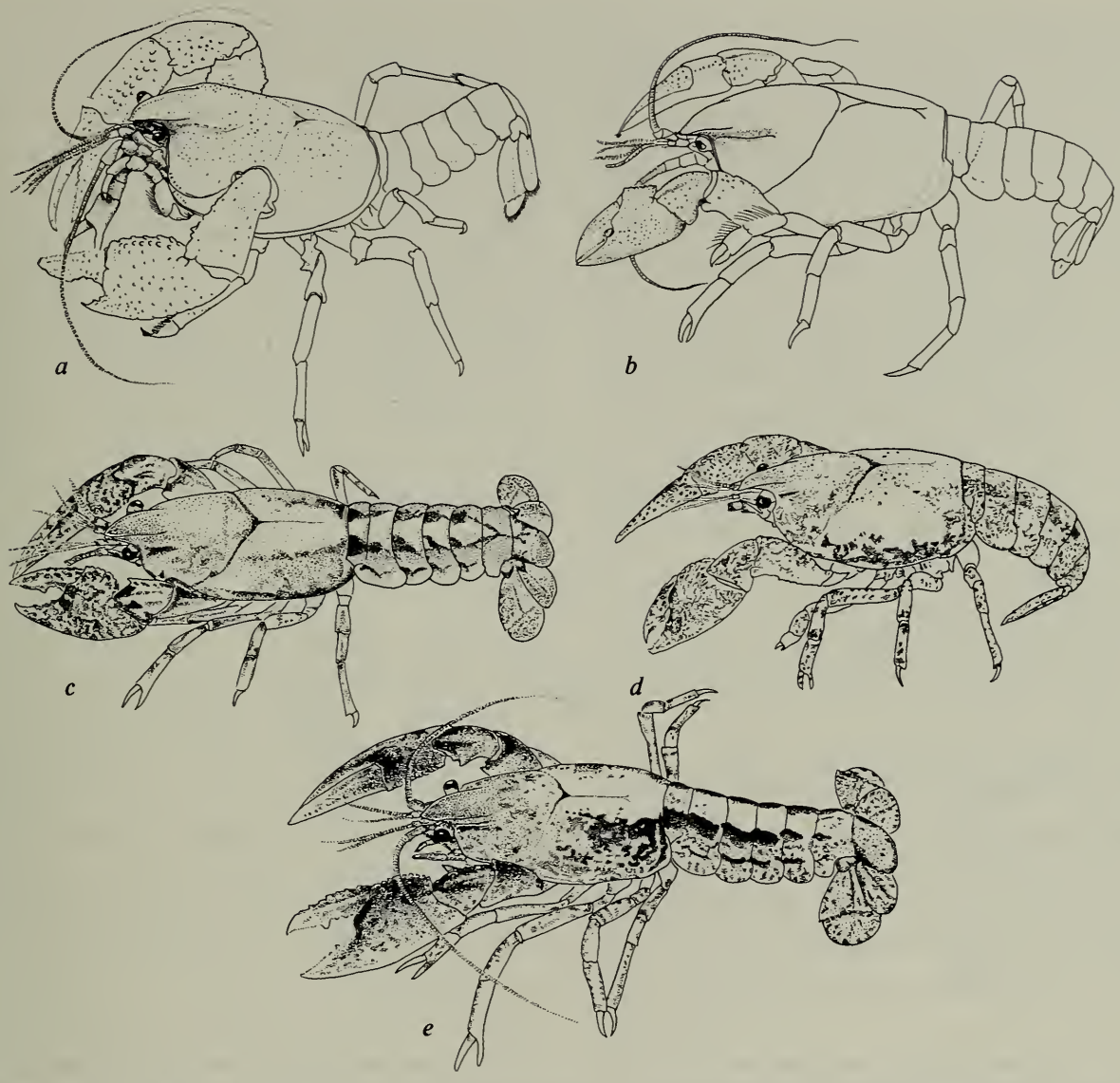

Fig. 4. Dorsolateral views of *Fallicambarus*: a, *F.* (*C.*) *petilicarpus*; b, *F.* (*F.*) *gilpini*; c–e, *F.* (*C.*) *fodiens* from: c, Independence County, Arkansas; d, Santa Rosa County, Florida; e, Orangeburg County, South Carolina.

Fallicambarus caesius.—Hobbs, 1975:28.—Bouchard & Robison, 1981:26.

Diagnosis.—Ventral surface of merus of cheliped with mesial row of tubercles, lateral one never represented by more than 2. Lateral margin of chela strongly costate, never serrate, dorsal surface without scattered tubercles in lateral half, ventrolateral surface with arched row of prominent punctations bearing long setae; opposable margin of dactyl with longitudinal row of tubercles extending along at least proximal third of finger. Mesial surface of palm of chela of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod without proximomesial spur, and lacking cephalic process; central projection weakly arched, its base not inclined laterally, its distal part directed caudoproximally, bearing well defined subapical notch, and never crossing central projection of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod somewhat rounded, neither strongly compressed nor conspicuously protruding ventrally. Mesial ramus of uropod with or without distolateral spine; distomedian spine premarginal. Telson incompletely divided and with or without spine on anterolateral flank of suture.

Range and specimens examined.—Insofar as is known, this crayfish is endemic to Arkansas where it is confined to the Oua-

Fig. 5. Distribution of *Fallicambarus* (*F.*) *harpi* (doubly encircled star); *F.* (*C.*) *caesius* (encircled dot); and *F.* (*C.*) *gilpini* (encircled star) in Arkansas. (Some localities listed in text for *F.* (*C.*) *gilpini* are too close to be noted on map.)

chita and Dorcheat Bayou basins in the southern part of the state. We have examined material from the following localities. Clark County: (1) Rose Hedge Cemetery at Gurdon, 1 ♀, 12 Mar 1983, HWR; 1 ♂ II, 1 ♀, Apr 1982, WL; 1 ♂ II, 1 ♀, 3 j♂, 1 j♀, 16 Apr 1983, DDK, HWR. Columbia County: (2) in Magnolia city limits, 1 ♀, 19 Mar 1984, J. Pesses. (3) Waldo, 1 ♀, 24 Aug 1981, EL. (4) seep 0.5 mi (0.8 km) W of Waldo at US Hwy 82, 1 ♀ with young, 17 Mar 1983, HWR. (5) seep 2 mi (3.2 km) W of Waldo at jct of Hwys 82 & 98, 4 ♀, 9 Apr 1983, HWR; 1 ♀, 3 j♂, 1 j♀, 2 ovig ♀, 11 Feb 1984, HWR; 1 ♂ I, 1 ♂ II, 7 ♀, 3 j♂, 3 j♀, 24 Feb 1984, HWR. (6) behind Impson Whitehead Veterinary Clinic in Magnolia, 1 ♂ I, 10 Nov 1979, M. Bryan. (7) Beene residence in Magnolia, 1 ♂ II, 22 May 1983, L. Robison. Dallas County: (8) 0.4 mi (0.64 km) N of Dallas-Ouachita Co line on St Rte 7, 1 j♂, 16 Apr 1983, HWR. Hempstead County: (9) Blevins, 1 ovig ♀, 11 Apr 1984, J. Tucker; 1 j♂, 1 j♀, 20 Apr 1982, EL; 5 j♀, 8 Mar 1984, E. McMullen. (10) Blevins, Sec 15, T10S, R24W, 2 ♀, 15 Mar 1984, B. Scott. (11) Blevins, Sec 11, T10S, R24W, 3 ♀, 15 Mar 1984, T. Taylor. (12) Bollins Bayou near Blevins, Sec 26, T9S, R24W, 1 juv, 25 Apr 1983, HWR. (13) Blevins, Sec 6, T10S, R24W, 1 ♂ II, 2 ♀, 20 May 1983, C. Webb. (14) Blevins, Sec 20, T10S, R23W, 1 ♂ I, 29

Apr 1983, T. Winn. (15) Blevins, Sec 16, T10S, R24W, 1 ♂ I, 2 ♀, 19 May 1983, B. Stephens. Hot Spring County: (16) roadside ditch 2.0 mi (3.2 km) W of Grant Co line on US Hwy 270, 3 ♀, 1 j♂, 30 Apr 1976, HHH & MK. Nevada County: (17) DeAnn Cemetery in Prescott, 2 ♀, 24 Nov 1980, K. W. Williams; 1 ♀, 10 Sep 1979, EL; 1 ♂ I, 16 Feb 1982, KWW; 1 ♂ I, 12 Apr 1980, KWW. (18) 3 mi (4.8 km) E of Rosston on St Rte 4, 2 ♂ II, 4 ♀, 6 j♂, 2 j♀, 8 Mar 1984, DDK. (19) 0.4 mi (6.4 km) from jct of St Rte 19 and Cale Rd, between Laneburg and Rosston, Sec 7, 8, T13S, R21W, 5 ♂ I, 4 ♀, 4 j♀, 15 Apr 1983, DDK. Ouachita County: (20) 0.9 mi (1.44 km) N of jct of US Hwy 79 and St Rte 203, 1 ♂ II, 26 Apr 1986, HWR. Saline County: (21) roadside ditch at Hot Spring County line on US Hwy 67 (Type locality), 1 ♂ I, 2 ♂ II, 1 ♀, 2 j♀ (Type series), 22 Apr 1973, GBH, JEP, HHH.

Color notes.—"(Based on freshly molted holotypic male.) Carapace bluish gray; dorsal thoracic region and large arrow-shaped area (with base between origins of mandibular [adductor] muscles and extending to apex of rostrum) darker and more bluish than lateral surfaces of branchiostegites, hepatic, and posterior gastric regions where more olive than blue. Cephalic section of tergum of first abdominal segment midnight blue, and caudal section slate blue; successive terga also slate blue but becoming progressively lighter in color posteriorly to tip of telson. Second through fifth terga with reticulate, but almost symmetrical, pattern involving oblique sublinear, dorsolateral grayish cream markings. Sixth tergum and telson with ornate symmetrical light markings. Uropods mostly very pale gray, but proximolateral parts somewhat darker with dark bluish splotches and dark median ribs. Antennae and pereiopods with powder blue reticulations. Antennular peduncle dark, antennal peduncle dark mesially and laterally, but broad submedian area of penultimate podomere and lamellar part of antennal scale very pale, lateral margin of scale dark. Cheliped with dorsodistal surface of merus, dorsal surface of carpus, dorsomesial surface of palm, dorsal surfaces of fixed finger, and dactyl powder blue; both fingers with white tubercles on opposable margin and yellowish cream along distal portion; lateral costa cream, and fingers terminating in brownish cornified tips; bluish color on all podomeres fading ventrally to very pale pinkish cream; articular membranes with dark pink suffusion. Dorsal surface of remaining pereiopods blue from merus distally; basal podomeres and ventral surfaces of all pereiopods and sternum cream. Distal end of dorsal side of merus and dorsum of carpus and propodus of third maxilliped with blue reticulations" (Hobbs 1975:27–28).

Size.—The largest specimen is a female from Nevada County having a cl of 31.4 (pol, 27.5) mm. The smallest and largest first form males have corresponding lengths of 21.1 (18.8) mm and 29.5 (26.4) mm, respectively. The smallest female carrying eggs or young has corresponding lengths of 27.2 (24.4) mm.

Life history notes.—First form males have been collected in February, April, May, and November. Ovigerous females were found in February and April; only one, having a carapace length of 28.4 mm, seemed to be carrying anything like a full complement of eggs: 35 with diameters of 2.1 to 2.3 mm; the diameters of the few eggs carried by the other two females were 2.0 or 2.1 mm.

Ecological notes.—In the type locality, this crayfish was collected from highly branching burrows in "rain soaked soil consisting of clay, organic material, and some gravel" (Hobbs 1975:28). As in many, if not most, of the other known localities, sedges and grasses were present in the immediate vicinity of the burrows or nearby, and none was taken from burrows more than one meter deep, most, if not all, of which opened to the surface through two or three chim-

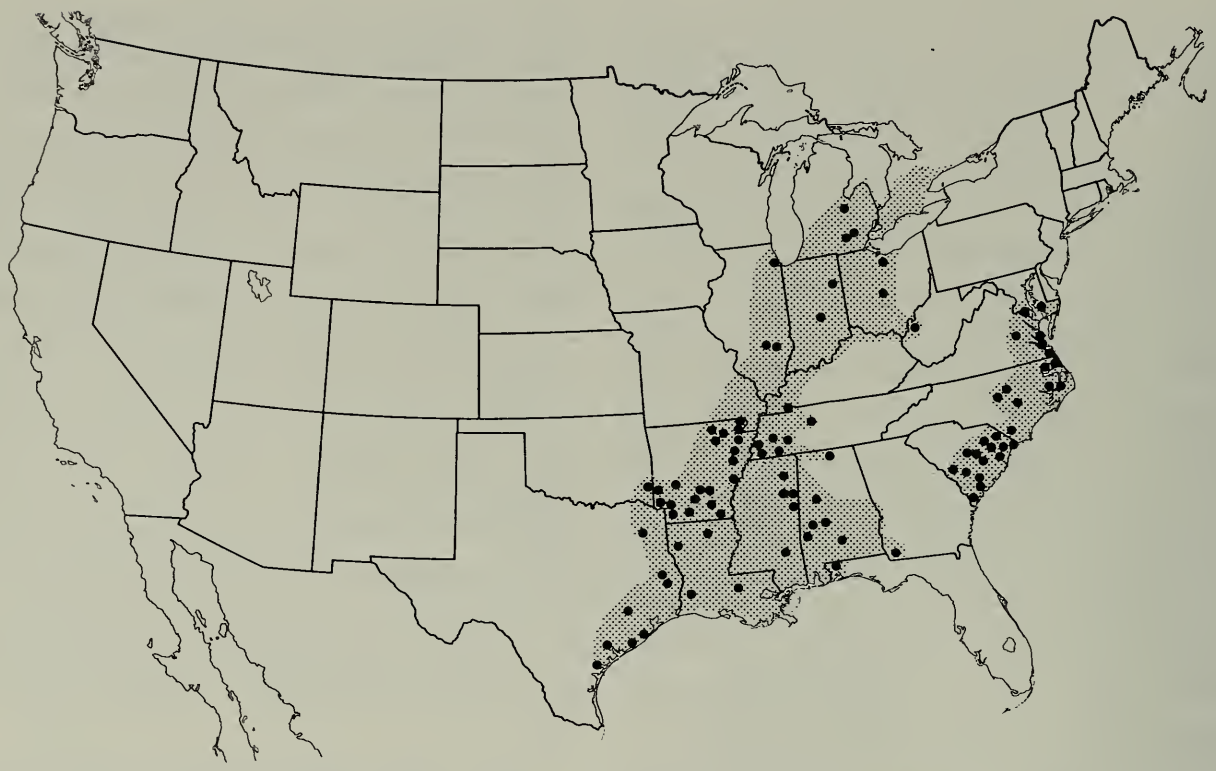

Fig. 6. Distribution of *Fallicambarus* (*C.*) *fodiens*. Dots mark localities represented by at least one first form male.

neys, and occasionally there was an opening to one of the galleries that was not marked by a turret.

Fallicambarus (*Creaserinus*)
fodiens (Cottle)
Figs. 1*b, o, s, t, u,* 6–9, 10*a–x*

Astacus fodiens (Cottle, 1863:217) [Types: not extant. Type locality: "Upper Canada," probably Ontario.].—Hobbs, 1969a: 111; 1973:463.—Bouchard, 1976b:586.—Page, 1985:422.

Cambarus obesus Hagen, 1870:82 [in part].—Faxon, 1885:71.—Osborn & Williamson, 1898:21.

Cambarus argillicola Faxon, 1884:115, 116, 144; 1885:56, 72, 76–78, 160, 174, pl. IV: fig. 2; 1890:624–625; 1898:650, 690; 1914:391, 400, 424, 426.—Underwood, 1886:366.—Hay, 1891:147; 1896:478, 491–493; 1899:959, 962; 1919:232; 1920: 83.—Stebbing, 1893:208.—Osborn & Williamson, 1898:21.—Williamson, 1899:48.—Harris, 1901:191; 1903a:59, 71–72, 105, 137, 139–140, 142–144, 146, 147, 150–155; 1903b:603, 605, 608.—Ortmann, 1902:277, 280, 283; 1905:120, 123, 136; 1907:712.—Pearse, 1910a:10, 11, 15, 19, 20, pl. VII; 1910b:73; 1911: 130.—Huntsman, 1915:158.—Cahn, 1915:136, 174.—Cummins, 1921:28–30.—Engle, 1926:89, 93, 94, 97, 98.—Turner, 1926:146, 154, 156, 160–163, 168, 169, 178, 186–188, 192.—Creaser, 1931:263; 1932:336.—Lyle, 1937:2, 16; 1938:76.—Brimley, 1938:503.—Bouvier, 1940:71.—Hobbs, 1942:165; 1948: 223, 224, 229, 230.—Rhoades, 1944: 98.—Bovbjerg, 1952:34.—Eberly, 1955: 283.—Crocker, 1957:90.—Hobbs & Hart, 1959:187.—Penn & Marlow, 1959:195.

Cambarus uhleri Faxon, 1884:116–117, 145 [Types: holotype, MCZ 3,624; paratypes, MCZ 3,633, 3,635, 3,636. Type locality: "Swamp on Eastern Road near Felsbury, Somerset County, Maryland" (restricted by Faxon, 1914:426).]. Faxon, 1885:22, 59, 77–78, 160, 166, 173, pl. VIII: figs. 8, 8′, 8a, 8a′.—Underwood, 1886:373.

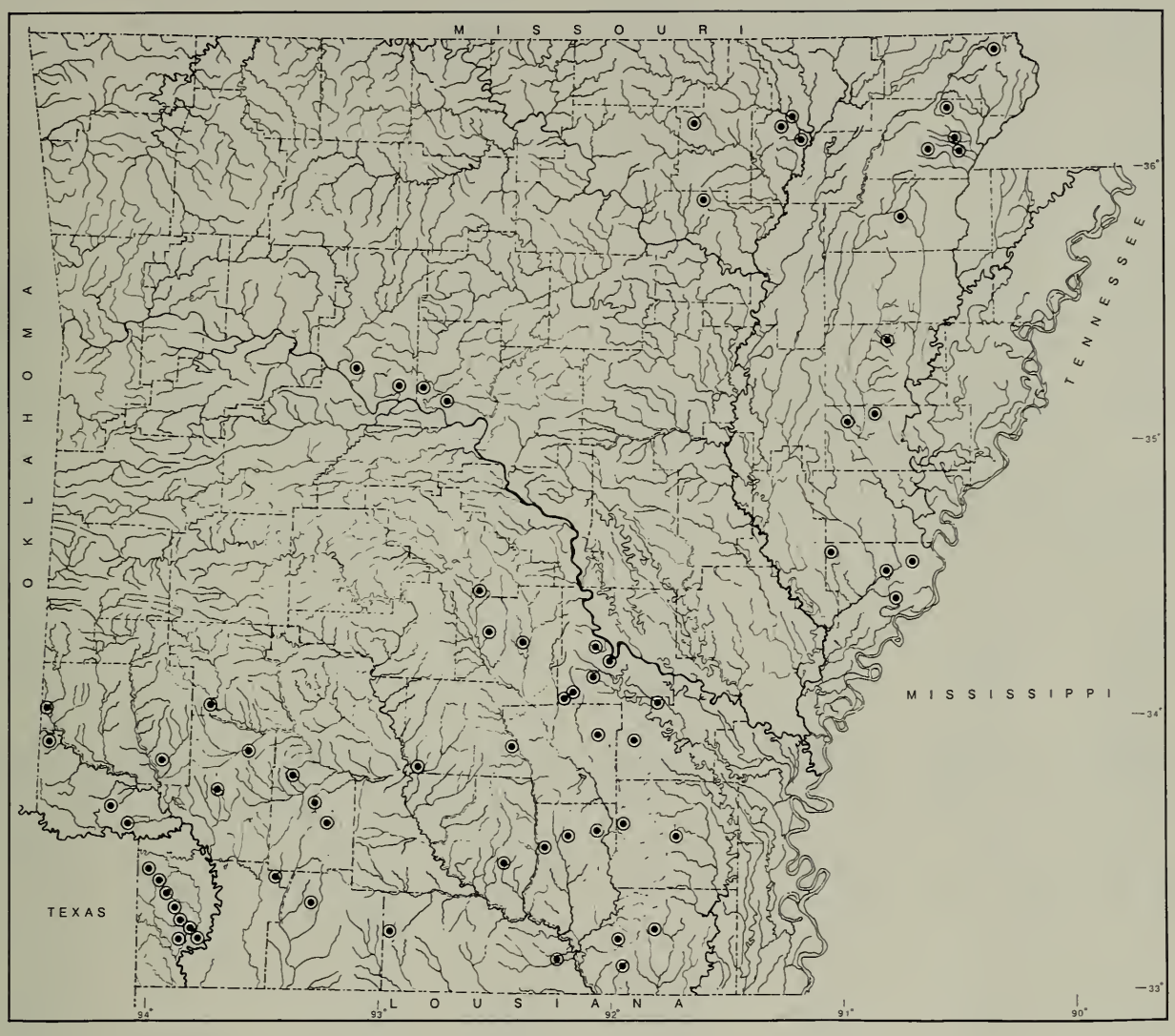

Fig. 7. Distribution of *Fallicambarus* (*C.*) *fodiens* in Arkansas.

Cambarus diogenes.—Faxon, 1885:71 [in part].

Cambarus uhleri.—Hay, 1899:959, 962; 1904:165.—Ortmann, 1902:277, 315; 1905:119, 123, 128.—Harris, 1903a:59, 80, 131, 138, 141, 142, 152, 158; 1903b: 606.—Williamson, 1907:755.—Fowler, 1912:568.—Faxon, 1914:400, 426.—Hay & Shore, 1918:401, pl. 28: fig. 6.—Creaser, 1931:269.—Brimley, 1938:503.—Hobbs, 1942:165; 1948:229; 1955:95, 98; 1959:896; 1966a:68, 70, 71; 1966b:115; 1968:K16; 1981:270.—Penn, 1955:73.—Crocker, 1957:69, 90.—Crawford, 1959: 150, 151, 177.—Meredith & Schwartz, 1959:2; 1960:4, 5, 21, 23, 27, 28, 30; 1962: 2.—Hoffman, 1963:330.—Miller, 1965: 43.—Hobbs III, 1969:42.—Hart & Hart, 1974:73, 91.—Holt, 1973:93.—Pickett & Sloan, 1979:26.—Andolshek & Hobbs, 1986:18.

Cambarus (*Bartonius*) *argillicola.*—Ortmann, 1905:120.

Cambarus (*Bartonius*) *uhleri.*—Ortmann, 1905:120.

Bartonius argillicola.—Williamson, 1907: 749, 752, 755, 758, 762, 763.

Cambarus (*Cambarus*) *uhleri.*—Fowler, 1912:341 [by implication].

Cambarus fodiens.—Huntsman, 1915: 158.—Creaser, 1931:263; 1932:336.—Hobbs, 1941:121; 1942:165, 167; 1948: 223, 224, 226, 229, 230; 1955:95, 98; 1959:896; 1966b:115; 1968:K16.—Penn, 1941:8; 1955:73, 80, 81.—Rhoades, 1942: 3; 1944:98; 1948:18; 1950:2, 3, 5; 1961: 2, 4.—Hobbs & Marchand, 1943:6.—Bovbjerg, 1952:34–36, 40–54; 1970:

Fig. 8. Mesial view of first pleopods of *Fallicambarus* (*F.*) *fodiens* from following counties in Michigan: a, Saginaw; b, c, Washtenaw. Indiana: d, e, Wells; f, Marion. Illinois: g, Cook; h, Jasper; i, Clark; j, Effingham; k, l, Richland. Ohio: m, Erie; n, Franklin. West Virginia: o, Mason. Arkansas: p, q, Lawrence; r, Sharp; s, Clay; t, u, Greene; v, Craighead; w, x, Independence; y, Cross; z, St. Francis; a′, Phillips; b′, Grant; c′, Jefferson; d′, e′, f′, Dallas.

232.—Pennak, 1953:464.—Eberly, 1954: 59; 1955:283.—Williams, 1954:810, 900, 902, 912, 918.—Spoor, 1955:77.—Crocker, 1957:90.—Penn & Hobbs, 1958: 482.—Hobbs & Hart, 1959:149, 151, 159–161, 164, 169, 171, 185, 187–188, fig. 11.—Hart, 1959:204.—Penn & Marlow, 1959:195, 202.—Wiens & Armitage,

Fig. 9. Mesial view of first pleopods of *Fallicambarus* (*F.*) *fodiens* from following counties or parishes in Arkansas: a, Ashley; b, Bradley; c, Columbia; d, Miller; e, Little River; f, Sevier. Oklahoma: g, McCurtain; Texas: h, Upshur; i, Angelina; j, k, Jasper; l, Brazos; m, Brazoria; n, Madagorda; o, Victoria; p, Aransas. Louisiana: q, De Soto; r, Ouachita; s, Calciseau; t, East Baton Rouge. Tennessee: u, Tipton; v, Crockett; w, Shelby; x, y, Hardeman; z, Cheatham. Mississippi: a′, Lee; b′, Clay; c′, Oktibbeha; d′, Lowndes; e′, Noxubee; f′, Jones.

1961:39–54.—Bowler, 1963:128.—Mobberly, 1965:45.—Judd, 1968:1–4, 6, 8.—Crocker & Barr, 1968:VIII, 12, 15, 29, 33, 35–37, 40, 56, 58–60, 125, 127, 129–135, 139, figs. 28, 37, 46, 57, 62, 85.—Fitzpatrick & Payne, 1968:14.—Jaspers & Avault, 1969:637.—Waywell & Corey, 1970:1462–1464; 1972:294–298.—Bell,

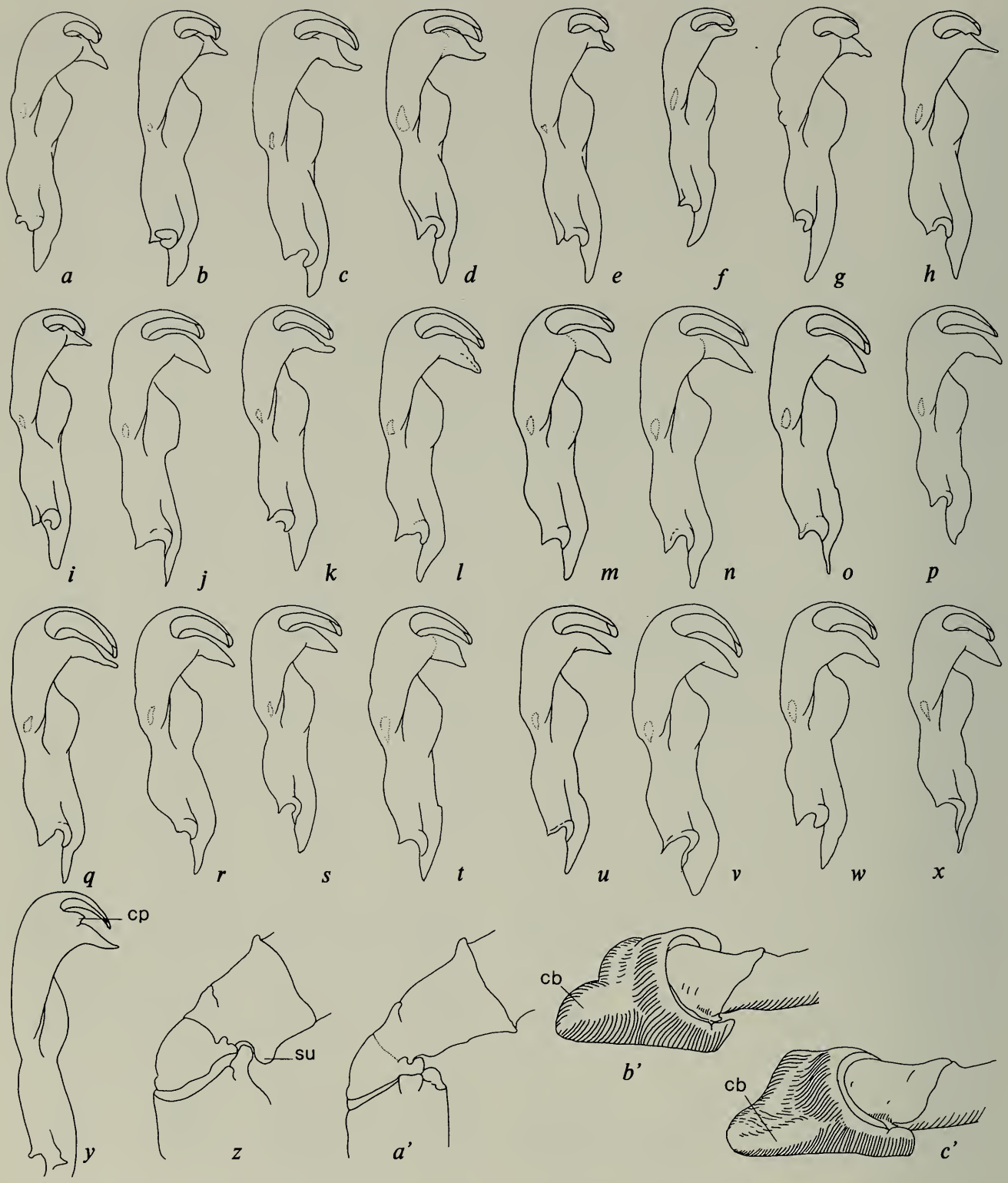

Fig. 10. (All illustrations from first form males.) a–x, Mesial view of first pleopods of *Fallicambarus* (*F.*) *fodiens* from following counties in Alabama: a, Lauderdale; b, Limestone; c, d, Tuscaloosa; e, Perry; f, Choctaw; g, Maringo; h, Butler. Florida: i, Santa Rosa. South Carolina: j, Beaufort; k, Bamberg; l, Colleton; m, Richland; n, Clarendon; o, Dillon; p, Marion; q, Horry. North Carolina: r, Columbus; s, Sampson; t, Hyde; u, Perquimines. Virginia: v, Norfolk; w, Warwick. Maryland: x, Dorchester. y, Same of *F.* (*F.*) *strawni* (cp, cephalic process); z, Lateral view of basal podomeres of cheliped of *F.* (*C.*) *fodiens* (su, sufflamen); a′, Same of *F.* (*F.*) *jeanae*; b′, Basal podomeres of fourth pereiopod of *F.* (*C.*) *burrisi* (cb, coxal boss); c′, Same of *F.* (*C.*) *gordoni* (cb, coxal boss).

1971:17.—Hobbs & Hall, 1974:200.—Terman, 1974:33, 34.—Williams, Williams, & Hynes, 1974:365–369, figs. 1, 2.—Caine, 1974:2.—Becker, Genoway, & Merrill, 1975:384.—Gladwell, Bowler, & Duncan, 1975:89.—Lake, 1977:59.—Berrill, 1978:166.—Momot, Gowing, & Jones, 1978:18.—Radaj, 1978:1.—Reinert, 1978:8.—Lawton, 1979:6.—Pickett & Sloan, 1979:26.—Bousfield, 1979: 292.—Crenshaw, Lemons, & Russo, 1980:245.—Grow & Merchant, 1980: 234.—Grow, 1981:355.—Kiley & Dineen, 1982:212.—Maude & Williams, 1983:68, 74, 76, figs. 6, 7.—McMahon & Wilkes, 1983:133.

Cambarus (*Bartonius*) *fodiens.*—Creaser, 1931:260, 261, 263, 269–272, fig. 37.

Cambarus hedgpethi Hobbs, 1948:224–230, figs. 17a–f, h–j, l [Types: holotype, morphotype, USNM 85146 (♂ I, ♂ II), and allotype, USNM 85147 (♀); paratypes, USNM. Type locality: lower middle part of Aransas National Wildlife Refuge, Aransas Co, Texas.].—Washburn, 1953: 6.—Penn, 1953:74; 1955:73, 80; 1959:8, 14–17, figs. 9, 27, 46, 64, map 9.—Penn & Hobbs, 1958:454, 462, 465, 467, 471, 473, 476–478, figs. 11, 28, 42, 55.—Hobbs, 1959:896; 1966b:115; 1968: K16.—Penn & Marlow, 1959:195–197.—Hobbs & Barr, 1960:13.—Reimer, 1966: 14; 1969:50, 51, 53, 60, 61, figs. 2, 39.—Black, 1967:176; 1969:197.—Walls & Black, 1967:60.—Fitzpatrick & Payne, 1968:14, 20.—Walls, 1968:417.—Hobbs III, 1969:19, 21, 26, 49, 64, tab. 2.

Cambarus hedgepethi.—Walls & Black, 1967:60 [erroneous spelling].

Fallicambarus fodiens.—Hobbs, 1969a:111, 112, fig. 20e; 1972:102, 137, figs. 5u, 82b, 83c, 84b, 85b; 1974a:12; 1974b:23, fig. 82; 1976:551, fig. 2d.—Hobbs & Fitzpatrick, 1970:835.—Bouchard, 1972:52, 62, 63, 107; 1976a:14; 1976b:585, 586.—Hobbs & Barr, 1972:9.—Hart & Hart, 1974:30, 31, 128.—Hobbs & Hall, 1974: 200, 201, 203.—Page, 1974:99; 1985:335, 336, 341, 343, 344, 350, 353, 422–426, 436, figs. 155–158.—Phillips, 1980:84.—Grow, 1981:355.—Bouchard & Robison, 1981:26, 27.—Huner & Barr, 1981:47; 1984:42.—Berrill & Chenoweth, 1982: 199.—Burr & Hobbs, 1984:14, 15, 16.—Norrocky, 1983:3.—Fitzpatrick, 1986: 126, 137.

Fallicambarus uhleri.—Hobbs, 1969a:111, 112, fig. 20j; 1972:102, 147, figs. 82a, 83b, 84a, 85a; 1973:463, 480, figs. 3d, 4; 1974b: 24, 101, fig. 84; 1976:551, fig. 1a.—Hobbs & Fitzpatrick, 1970:835.—Peters, 1971: 100; 1974:74; 1975:7, 22, 23.—Hart & Hart, 1974:22, 28, 33, 73, 129.—Hobbs III, Thorp, & Anderson, 1976:24.—Hobbs & Peters, 1977:6, 9, 12, 13, 19, 20, 21, 33, 43, 46, 49, 53, 54, 60, 61, 62.—Wharton, 1978:50.—Page, 1985:422.—Fitzpatrick, 1986:126, 137, 138.

Fallicambarus hedgpethi.—Hobbs, 1969a: 111, 112, 173, fig. 20f; 1969b:335; 1972: 102, 147, figs. 82c, 83d; 1974b:23, 100, fig. 83.—Hobbs & Hobbs, 1970:12, 14.—Hobbs & Fitzpatrick, 1970:835.—Bouchard, 1972:56, 62, 63, 107; 1977:11.—Albaugh, 1973:6, 11, 12, 25, 103.—Albaugh & Black, 1973:183, 184, 185.—Payne & Riley, 1974:125–127.—Hart & Hart, 1974:23, 93, 94, 97.—Reimer & Clark, 1974:168, 175, figs. 27–30.—Reimer, 1975:24.—Lahser, 1976:278, 279, 281–284.—Huner, Meyers, & Avault, 1976:150, 152.—Bouchard & Robison, 1981:26, 27.—Huner & Barr, 1981:57, 58; 1984:50.—Rogers & Huner, 1983:79; 1984:37; 1985:23, 24, 26–28, figs. 3, 4, 5.—Burr & Hobbs, 1984:15, 16.—Walls, 1985:193.—Page, 1985:424.—Fitzpatrick, 1986:137.

Fallicambarus (*Creaserinus*) *fodiens.*—Hobbs, 1973:463, 480, figs. 3g, 4.—Bouchard, 1976a:14; 1976b:586.—Clark & Rhoades, 1979:238, fig. 1.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983: 168, 169, fig. 175.—Thoma & Jezerinac, 1982:136, 137.—Jezerinac & Thoma, 1984:120–124, fig. 1.—Norrocky, 1984:

65.—Page, 1985:335.—Jezerinac, 1986: 178.—Jezerinac & Stocker, 1987:46, fig. 1.—Hobbs III & Jass, 1988:3, 23, 39–43, 141, 142, figs. 30, 31.—Mansell, 1989.

Fallicambarus (*Creaserinus*) *uhleri.*—Hobbs, 1973:463, 480, figs. 3d, 4.—Hobbs & Peters, 1977:6, 9, 12, 13, 19, 20, 21, 33, 43, 46, 49, 53, 54, 60, 61, 62.—Fitzpatrick, 1983:168.—Cooper & Ashton, 1985:9, 10.—Andolshek & Hobbs, 1986: 24.

Fallicambarus (*Creaserinus*) *hedgpethi.*—Hobbs, 1973:463, 480, fig. 4.—Bouchard & Robison, 1981:28.—Fitzpatrick, 1983: 169.

P[*rocambarus*] *Fallicambarus fodiens.*—Hart & Hart, 1974:88 [lapsus].

Fallicambarus hedgepethi.—Huner, 1977:11 [photo in color].

Fallicambarus sp.—Huner, 1978:621.

Fallicambarus (*Creserineus*) *fodiens.*—Jezerinac, 1983:5 [erroneous spelling].

Diagnosis.—Ventral surface of merus of cheliped with mesial and lateral rows of tubercles; length of carpus less than, or subequal to, width of palm of chela. Chela with lateral margin costate to rounded, never serrate, dorsal surface without scattered tubercles in lateral half, ventrolateral surface lacking arched row of prominent setiferous punctations; opposable margin of dactyl with distinct excision in basal half, mesial margin with longitudinal row of tubercles extending along at least basal third of finger. Mesial surface of chela of second pereiopod with conspicuous tufts of plumose setae. First pleopod without proximomesial spur and lacking cephalic process; central projection comparatively weakly arched, base not inclined laterally, distal part directed caudally, with or without subapical notch, but never crossing central projection of corresponding pleopod. Hooks on ischia of third pereiopods only. Boss on coxa of fourth pereiopod somewhat rounded, neither strongly compressed nor conspicuously protruding ventrally. Mesial ramus of uropod with distolateral spine; distomedian spine premarginal. Telson divided and with spines on anterolateral flank of suture.

Range and specimens examined.—From southern Ontario southwestward to Aransas County, Texas, and southeastward to the Apalachicola Basin, also present in the Coastal Plain and lower Piedmont from Beaufort County, South Carolina, to Somerset and Dorchester counties, Maryland (Figs. 6, 7). Engel (1926:93) recorded it from Lincoln, Nebraska, but this locality is so far removed from any other reported for the species that it must be confirmed. We have examined some 2500 specimens from Michigan (45), Indiana (58), Illinois (42), Missouri (20), Arkansas (420), Oklahoma (13), Texas (223), Ohio (50), West Virginia (2), Kentucky (58), Tennessee (130), Louisiana (29), Mississippi (143), Alabama (207), Florida (14), Georgia (15), South Carolina (451), North Carolina (386), Virginia (209), and Maryland (30).

Color notes.—In this crayfish, there seem to exist two basic colors and three color patterns, with a wide range of variation linking them. Most of the animals that we have seen are either predominantly tan with brown markings or olive-green with dark grayish to brownish green markings. The lighter ventral and ventrolateral areas may be almost white, cream, yellowish, pink, or lavender. Occasionally we have encountered individuals that are predominantly blue.

As for the color patterns, the striped (Fig. 4*c, e*) is the most common. In it, clearly defined longitudinal stripes, that are usually most obvious on the abdomen, make this pattern conspicuously different from the least common concolorous one. The latter is typified by the absence of stripes, splotches, or specks. Decidedly more common than the concolorous pattern is the speckled one (Fig. 4*d*; often the specks and splotches are much more abundant, especially dorsally, than depicted) in which the carapace and abdomen are marked dorsally by specks and

irregular dark spots scattered over a lighter background. Paired dorsolateral concentrations of darker pigment, which are often more diffuse than in Fig. 4*d*, on the abdominal terga no doubt represent remnants of the dark stripes that are so conspicuous in the striped pattern. In specimens exhibiting concolorous patterns, which are not illustrated, the dorsum of the cephalothorax is an almost uniform dark brown, green, or blue, fading laterally to cream or very light gray. The abdominal terga, too, are almost uniformly dark brown, green, or blue almost to their junctures with the pleura, which, together with the uropods, are of a much diluted hue of the color of the dorsum.

All three patterns have been observed repeatedly among specimens collected in a single locality, the most recently seen were in a collection from western Sevier County, Arkansas, less than a mile from the Oklahoma line.

Hay (1904:165) remarked that the specimens from Maryland were "a dirty greenish brown, the tips of the chelae alone being somewhat reddish." He reported further that Uhler, who first collected the species in Maryland, related to him the presence of beautiful yellow spots. While we have not observed the latter, we have encountered specimens with cream, yellow, orange, and red tipped chelae, but we have not associated any of these colors with a particular geographic region.

Size.—The largest specimen of this species that we have examined is a first form male from Richland County, Illinois, which has a cl of 42.8 (pol 36.7) mm. The smallest first form male (from Perquimens County, North Carolina) that we have seen has corresponding lengths of 19.5 (16.0) mm. Those of the largest and smallest from Arkansas are 36.4 (32.4), from St. Francis County, and 22.8 (19.2) mm, from Dallas County. Comparable measurements of the smallest female carrying eggs or young that we have seen are 26.5 (22.6) mm; this specimen was collected in Columbia County, Arkansas.

Life history notes.—Considering populations throughout the range of the species, first form males have been collected during every month of the year; ovigerous females were found from January to June and in September, October, and November, and females carrying young from January to April and in September. In Maryland, this crayfish was reported by Hay (1904) to leave its burrows in the spring when it becomes common in ditches and small streams. Finding both first and second form males in September led him to conclude that the transition in males from form II to form I must occur in the late fall.

The data for Arkansas are indeed inadequate; except for a total of 11 members of the species collected in June, July, and November, all of the material from the state available to us was collected during February (11), March (31), April (250), and May 15). Among the collections from the state, there are first form males collected in February, March, April, May, and November, ovigerous females in February, April, and November, and others carrying young in January, February, and March.

The egg complements of three of the ovigerous females appear to be reasonably complete and are as follows: cl 28.2, pol 24.8 mm, 190 eggs; cl 28.2, pol 24.2 mm, 196 eggs; cl 26.5, pol 22.6 mm, 177 eggs. The diameters of the eggs were 1.9 and 2.0 mm.

Ecological notes.—Ecological data that have been recorded pertaining to *F. (F.) fodiens* were recently summarized by Hobbs III & Jass (1988:41–43). The following discussion is therefore limited to a few recorded observations on the eastern facies of *Fallicambarus (C.) fodiens* (formerly *F. (C.) uhleri*) and to those made by us on the presence of this crayfish in Arkansas, where it frequents temporary pools and burrows from the floodplains of the major rivers to the foothills of the Ozark and Ouachita mountains. According to Faxon (1884:117), his *C. uhleri* occurs in "salt marshes, covered twice daily by the tides, and also in brackish

and fresh-water ditches. . . ." On the eastern shore of Maryland, Hay (1904:165) found it to be "rather abundant in burrows in low-lying areas not far from the bay but always near ponds or ditches of freshwater. In nearly every case the area selected was in dense pine woods." Hay also learned from local inhabitants of the area that in the spring the crayfish "emerge from their burrows and are common in ditches and small streams." The original collection of the species taken by Dr. Philip Uhler was made partly in water that was distinctly brackish.

In Arkansas, this crayfish is primarily an inhabitant of temporary bodies of water and burrows, although occasionally it ventures into more permanent lentic and lotic habitats. Apparently wherever it occurs in the State the water table must be within range of its burrowing capabilities, for we have no evidence that any members of the species undergo a life-span devoid of periods of what is an apparently voluntary fossorial existence. Whereas we have retrieved a few specimens from burrows that did not penetrate the water table, most were taken from pockets of water in them at depths of 0.5 to 1.5 meters. The external appearance of these burrows is described in the introductory remarks where it was also pointed out that those excavated by members of this species are comparatively simple. Most consist of a subvertical passageway, in clay, sandy clay, or sandy loam, opening to the surface through one or two apertures that may or may not be surrounded by low, for the most part poorly formed, chimneys, and at the fundus of the passageway there is a slight enlargement. Occasionally we have encountered a burrow with a second subvertical gallery leading downward from the main one. With little doubt, these simple I-, Y- or X-shaped patterns reflect, in part, physical features of the environment involving the availability and retention of water. In habitats where there is evidence (based on the presence of hydrophytic plant communities) that during much of the year the water table is close to the surface, this species is largely confined to the marginal areas, and another (e.g., *F.* (*C.*) *caesius* or *F.* (*C*) *gilpini*) dominates, with its shallow, dendritic systems of galleries, the more permanently wet parts of the seasonal seeps. The burrows of those individuals that invade the wetter areas do branch more than those we have regarded as more typical. Clumps of sedges frequently mark the sites of temporary stands of water, and areas in which a not-too-deep retreat of the water table occurs, features that together provide what appears to be the favorite habitat of the species in Arkansas.

Most of the burrows that we have dissected contained a single individual, occasionally one inhabited by a female and a first form male, and sometimes one housing a female with young either clinging to her abdomen or sometimes with young that are presumed to have abandoned their mother. We have no information as to the permanency of habitation of a domocile by an individual. Until the current study of J. Norrocky (manuscript in preparation) involving marking and recapturing members of the species in Ohio, we were almost convinced that a female was a nearly permanent resident of the burrow she occupied, never wandering far away. This assumption was made, at least in part, on the basis of the size of the turrets marking the entrance/s. There can be little doubt that the larger turrets mark the burrows inhabited by the larger females, and there is no question that the more massive chimneys reflect more spacious and deeper domiciles. These observations suggested to us the probability that the older, larger, females had spent a longer time enlarging and reworking their domiciles than had the smaller females and males, probably spending the better part of their entire lives hauling soil pellets to the surface. In light of some of Norrocky's data (personal communication) there is good reason to question our conclusion as to the tenure of an individual in a single lair. While

the males must have their own burrow at the time of their presumed biannual molts, there is good reason to believe that when in form I they abandon their burrows, at least temporarily, for sojourns in the domains of one or more females that might be visited. The question as to whether or not they return to their homestead following the breeding season or seek seclusion elsewhere remains unanswered.

Following rains, when pools flood the mouths of the burrows, the juvenile element of the population emerges in numbers and small crayfish may be observed wandering hither and yon, even during daylight hours. An occasional adult also appears in the open water, and, no doubt, many more adults leave their lairs for short forays in the pools at night, but most return to burrows by at least the early morning hours.

We are much puzzled by the paucity of colonies of this crayfish throughout most of the rice-growing areas of the state. Surely when the region was still wooded, and shallow temporary pools were common features of the landscape, numerous colonies of *F.* (*F.*) *fodiens* must have existed between the Arkansas and Mississippi rivers. Now, one must search rather diligently to find even an isolated burrow in much of the area under cultivation. It is understandable that a crayfish might have difficulty in remaining well established in fields that are subjected to the treatment accorded the cultivation of rice, but why should they not be present in the roadside ditches that border these vast tilled and alternately flooded and drained lands? In Cross County, for example, a careful search of the ditches along highways and secondary roads for miles revealed only one colony of this crayfish, though the lawn around one of the churches in Hickory Grove was pitted by scores of burrows that must have been constructed by members of this species. Not only is this crayfish largely absent where it should occur in numbers, but other species (*Procambarus* (*Ortmannicus*) *acutus acutus* (Girard, 1852), *Cambarus* (*Lacunicambarus*) *diogenes* Girard, 1852, and *C.* (*L.*) *ludovicianus* Faxon, 1914) are also encountered infrequently. It seems likely that something associated with the production of rice is affecting adversely the exploitation of the area by crayfishes.

We are further puzzled by our failure to find a single member of this species between the Arkansas and White rivers downstream from Pope County. We do not claim to have exhausted possibilities of the existence of overlooked colonies, but considerable effort has been expended along several routes traversing the area between the two rivers.

Remarks.—United here are three formerly recognized species which for a number of years have presented difficulties to one of us (HHH) in searching for characteristics that might be used in their differentiation (e.g., Hobbs 1959, 1972, 1973, 1981). In preparing an account of the *Fallicambarus* from the Apalachicola basin in his study of the crayfishes of Georgia, Hobbs (1981) assigned the specimens that he had previously identified as members of *Cambarus fodiens* (Hobbs & Hart, 1959:187) to *F. hedgpethi.* But before doing so he had vacillated between assigning them to one of the two and to describing them as new! Had the material subsequently collected in eastern Arkansas and from a number of other localities, as well, been available to him, it is likely that he would have arrived at the conclusions that have been reached in the current study.

Given specimens from the vicinity of the type localities of these three crayfishes, we do not believe that anyone would have difficulty in distinguishing between them: the first pleopod of the first form males of *F. fodiens* exhibits a much shorter central projection than do those of either *F. hedgpethi* or *F. uhleri,* and the latter has an areola that constitutes less than 39 percent of the length of the carapace whereas that of *hedgpethi* is more, and the opposable margin of the dactyl of the chela with two instead of one major tubercle is typical only of *F. hedgpethi*;

too, in the latter the arrangement of the tubercles on the mesial surface of the dactyl of the chela in two well developed rows differs from the usual single well developed row in the other two. The limited known range of *fodiens* when *uhleri* was described from Maryland by Faxon in 1884, and the existing poor concept of the distribution of the two when *hedgpethi* was found in southwestern Texas, gave neither Faxon nor Hobbs reason to question the validity of the seemingly distinctive characters that they chose in naming what we now believe to be peripherally located populations of a single species. These occur at the angles of a large, distorted, triangular range which in Pliocene, and probably in part of Pleistocene, times must have been continuous. The range appears even now to be unbroken except for a gap apparently existing across the southern part of Georgia where members of the subgenera *Hagenides* and *Leconticambarus* of the genus *Procambarus* are probably vicariating for *F. fodiens* (see Hobbs 1981: 317, 348).

Comparisons of the materials from throughout the range of the species have been made, and we have discovered only a few characters (those associated with the first pleopod of the first form male) that are geographically or ecologically restricted to a limited part of the range of the species. The measurements made of the carapace and chelipeds that have been translated into ratios suggest that some local populations are rather distinctive, but they, too, are not consistent for large segments of the range, and there are no indications of clinal trends. Until now, the *Fallicambarus* ranging along the Atlantic versant from South Carolina to Maryland has been identified as *F.* (*C.*) *uhleri*. In southern South Carolina the areola of this crayfish spans from 36 to 41 percent of the carapace length, in North Carolina from 34.8 to 38.7 percent, and in Virginia and Maryland 35.2 to 38.5 percent, and in several localities in South Carolina the ratio is distinctly above 39 percent. When these specimens from South Carolina are compared with others from the state, we find nothing else that will set them apart, and in the midst of their range there are specimens with areolae occupying as little as 36 percent of the carapace length. If the comparisons are extended to specimens from more western localities including those from Arkansas and Texas the ratios range from 32.7 in Cheatham County, Tennessee to 41.5 in Tuscaloosa County, Alabama, and Brazos County, Texas. Moreover, there seems to be no distributional pattern in the variations between these extremes.

Even the three color patterns (concolorous, speckled, and striped) that have been noted appear in a single population. Most of the specimens that we have examined from Illinois to Ohio and West Virginia northward possess chelae in which the opposable margin of the fixed finger bears one tubercle that is slightly to distinctly larger than the others, and the tubercles on the mesial surface of the dactyl are largely aligned in a single row. Specimens from the Atlantic versant exhibit, for the most part, similarly adorned chelae. In contrast, however, in most of those in the lower gulf coastal area, the fixed finger bears two large tubercles and those on the mesial margin of the dactyl form two well developed rows. In eastern Arkansas, Tennessee, and Alabama, these features appear in a haphazard fashion.

First pleopods of first form males from throughout the range of the species are depicted in mesial aspect in Figs. 8–10. On the basis of variations noted in specimens from Ontario (see Crocker & Barr 1968: fig. 28), Michigan, and Ohio to Aransas County, Texas (from Missouri southward only west of the Mississippi River), and were there no populations occurring east of the river, we should not hesitate to conclude that two subspecies of *F. fodiens* should be recognized. The nominate subspecies (distinguishable almost solely on features of the first pleopod of the first form male in which

the comparatively short central projection usually bears a subapical notch (Fig. 8*a–y*)) could be considered to occupy the northern sector, extending as far south as northern Arkansas, where throughout the eastern part of the state it intergrades (Figs. 8*z*–9*g*) with the more southwestern populations, ranging from southwestern Arkansas and southeastern Oklahoma southward. These more southern populations exhibit the facies that has been associated with *F. hedgpethi* (recognized by the possession of a long central projection lacking a subapical notch, Fig. 9*h–s*). It should be noted that an occasional influence of the *fodiens* genome surfaces in specimens occurring south of the Arkansas border (see Fig. 9*j, q*). East of the Mississippi River, we fail to find any such regular distribution pattern in the variation of pleopodal features (Figs. 9*t*–10*i*) except along the Atlantic versant from South Carolina to Maryland (Fig. 10*j–x*). But the same type pleopod that characterizes those populations occurring along the eastern seaboard may be found in specimens from Alabama and Texas (Fig. 9*j, t*). Thus, we have been unable to discover a single character that serves consistently to distinguish between the formerly recognized *F.* (*C.*) *fodiens, F.* (*C.*) *uhleri,* and *F.* (*C.*) *hedgpethi.* The two diagnostic features that Faxon (1884:117) mentioned as setting his *Cambarus uhleri* apart from *C. argillicola* (=*F. fodiens*) were its "plane rostrum [and] shape of the hand. . . ." Many specimens, particularly those from the Carolinas, have concave rostra, and while we are not certain as to which features in the "shape of the hand" Faxon was referring, there seems to exist as much variation within specimens from South Carolina to Maryland as we have noted in individuals from the rest of the range of the species, and we have recognized no feature as being unique. As noted above, the same applies to characteristics pointed out by Hobbs as typifying his "*Cambarus hedgpethi.*"

Notes on sex ratio.—In all of the studies of which we are aware that have yielded data on the sex ratios of cambarids except that of Creaser (1934) (e.g., Andrews 1904, Penn 1943, Smith 1953:92, and Smart 1962:94), all have revealed a near 1:1 ratio. Insufficient numbers of individuals of any population of members of the genus *Fallicambarus* in Arkansas have been available that might permit an estimate of the sex ratio in any population, but, in the samples at hand there are many more females than males. Most of our adult specimens of *Fallicambarus* (*F.*) *fodiens* were removed from burrows, and of 293 adults, less than half, only 98, are males. In order to support the belief that our data are little biased, we have repeatedly attempted to discover some way in which to determine whether a burrow to be excavated contains a male, female, or pair, but we have been unsuccessful. (As will become evident below, the importance of obtaining first form males from throughout the range of the species is paramount.) On 21 April 1973, in a seepage area 0.4 mile east of the Oklahoma State line on U.S. Highway 70, in Sevier County, Jean Pugh and HHH removed 23 females from burrows before they found a male. In Phillips County, on 17 April 1985, Robert Gilpin and HHH retrieved females from 14 burrows in one locality without finding a male, and, at another nearby, they unearthed five females before taking a male. Except for their apparent rarity, we are aware of no evidence that the males of *F.* (*F.*) *fodiens* might be more secretive than are the females; and, we suggest that perhaps two of their habits are responsible for the real or apparent absence of half of them (assuming the sex ratio at hatching is near 1:1) from the adult population. To a minor extent, perhaps our data are biased, for the burrows of the males seem sometimes to be less elaborate than those of the female, and this is reflected in the often smaller, open, and eroded turrets marking their domiciles. Admittedly, such burrows offer less temptation to the collector, who, for good reason, prefers to explore

one over which the turret is capped, or, if open, adorned with comparatively recently deposited, not abraded, pellets. Well-formed soil pellets offer evidence of the presence of a crayfish instead of perhaps a snake (*Agkistrodon piscivoris* or an ill-tempered *Nerodia sipidon*), an *Amphiuma,* or some other invader. At one time we suspected that of more importance in skewing the apparent sex ratio of adults than failure of collectors to excavate burrows harboring males are the supposed more frequent wanderings of first form males in seeking mates. In their forays from one lair to another, they place themselves in jeopardy of becoming prey to raccoons, skunks, owls, and other predators, and indeed scat from owls and raccoons has been observed to contain fragments of the exoskeleton of crayfishes within the range of the species in Arkansas. Thus by their being more frequently exposed to predators than are females, we reasoned that they are being passively selected, and perhaps effectively so. What significance, if any, attaches to our having observed more carcasses of first form males than females of this species in areas where their burrows are located escapes us.

We had placed considerable confidence in the above suggestions as possible explanations for the apparent skewed sex ratio existing in the adult populations of *F. fodiens* until, on 22 April 1988, one of us (HWR) collected 30 juveniles (cl 5.5 to 11.5 mm) of this species from a pool in the ditch at the locality mentioned above where Pugh and Hobbs had collected in 1973. Twenty-nine of the specimens were females! The question remains as to whether or not the sex ratio at hatching in this species is 1:1, and if it is what factor/s (cannibalism of the perhaps slower growing juvenile males—the male is the smallest of the 30 juveniles) are responsible for the subsequent alteration of the ratio. That our suppositions might well be suspect seem possible when we remembered Creaser's (1934) study revealing possible seasonal changes in populations of the lake- and stream-dwelling *Faxonius* (=*Orconectes*) *propinquus* in which from August to January 66 to 73 percent of the population was female; during the rest of the year the percentage ranged from 43 to 56 percent. Creaser was apparently as puzzled by these data as are we by the information we have on *F.* (*C.*) *fodiens.*

Fallicambarus (*Creaserinus*) *gilpini,* new species

Figs. 1*q,* 5, 11

Diagnosis.—Cheliped with sufflamen; ventral surface of merus with mesial row of tubercles, lateral one never represented by more than two; length of carpus less than or subequal to width of palm of chela. Chela with lateral margin strongly costate, never serrate, dorsal surface lacking scattered tubercles in lateral half, ventrolateral surface with arched row of prominent punctations bearing long setae, opposable margin of dactyl with distinct excision in basal half, mesial margin without tubercles. Mesial surface of palm of second pereiopod lacking conspicuous tufts of plumose setae. First pleopod lacking proximomesial spur, and lacking cephalic process; central projection weakly arched, its base not inclined laterally, its distal part directed caudoproximally with well defined subapical notch, never crossing central projection of corresponding pleopod. Hooks present on ischia of third pereiopods only. Boss on coxa of fourth pereiopod somewhat rounded, not distinctly compressed. Mesial ramus of uropod with distolateral spine; distomedian spine premarginal. Telson incompletely divided, with spine on anterolateral flank of suture.

Holotypic male, form I.—Eyes small but pigmented and with faceted cornea. Body subcylindrical, very weakly compressed (Figs. 4*b,* 11*a,* l). Abdomen distinctly narrower than thorax (7.3 and 10.1 mm). Greatest width of carapace at level about one-third length of areola from cervical groove where subequal to height (10.1 and

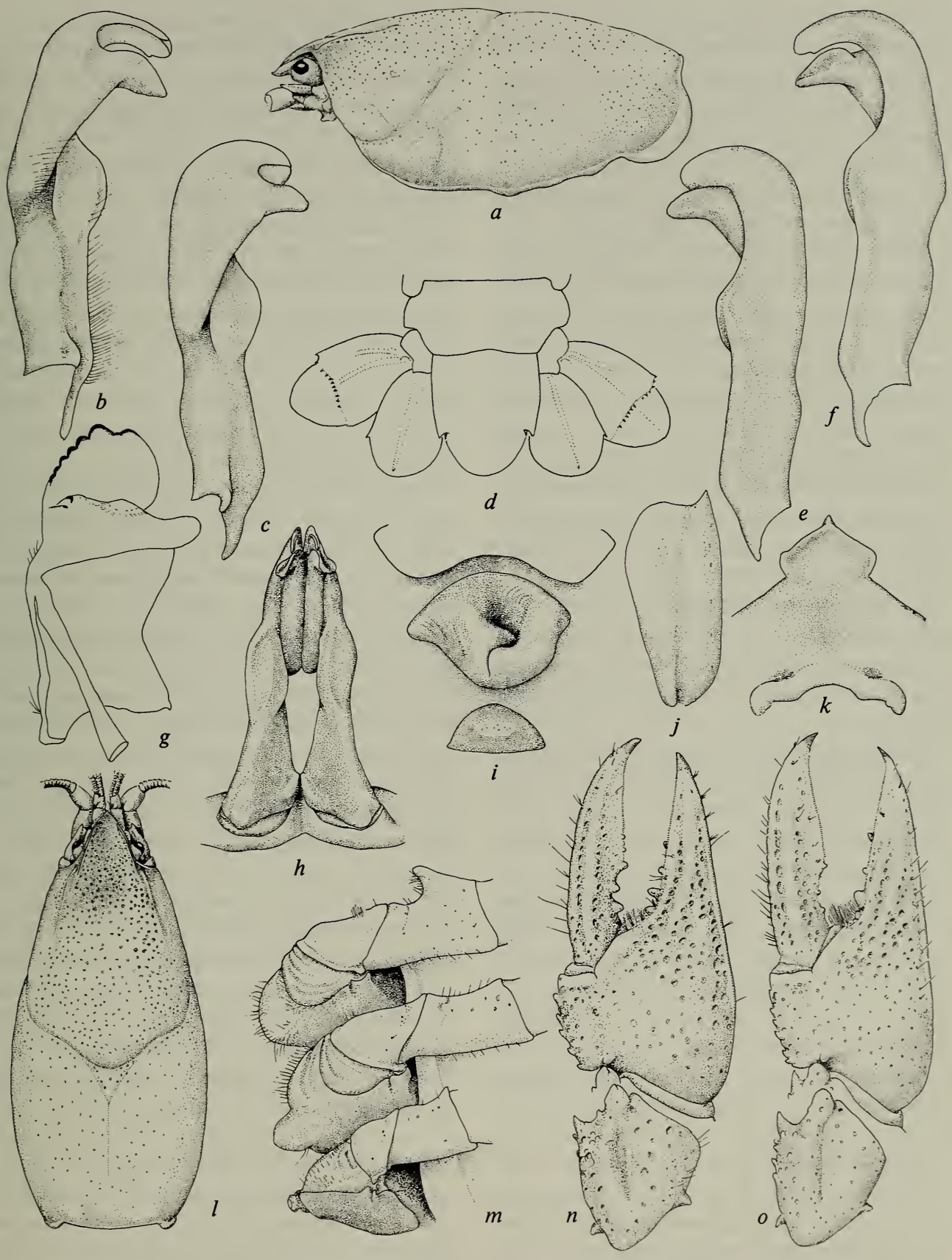

Fig. 11. *Fallicambarus* (*Creaserinus*) *gilpini* (all from holotype except c, e, from morphotype, and i, n from allotype): a, Lateral view of carapace; b, c, Mesial view of first pleopod; d, Dorsal view of caudal part of abdomen; e, f, Lateral view of first pleopod; g, Postaxial view of mandible; h, Caudal view of first pleopods; i, Annulus ventralis and associated sclerites; j, Antennal scale; k, Epistome; l, Dorsal view of carapace; n, Basal podomeres of third, fourth, and fifth pereiopods; n, o, Distal podomeres of cheliped.

10.0 mm). Areola linear over most of length and comprising 40.5 percent of entire length of carapace (46.6 percent of postorbital carapace length). Rostrum with convergent, slender margins gently contracted anteriorly, marking base of poorly delimited acumen, apex corneous, slightly upturned, and reaching base of ultimate podomere of antennular peduncle. Dorsal surface of rostrum concave with submarginal rows of setiferous punctations and others between, especially dense and conspicuous in basal part. Subrostral ridges weak but evident in dorsal aspect to base of acumen. Postorbital ridges slender but well defined and merging almost imperceptibly with carapace above posterior margin of orbit. Branchiostegal and cervical spines absent. Suborbital angle absent, cephalolateral margin of carapace sloping caudoventrally from base of rostrum without excrescence or excision. Carapace comparatively densely punctate dorsally and laterally; row of few small tubercles flanking anterolateral segment of cervical groove.

Abdomen (Fig. 4*b*) shorter than carapace (19.8 and 22.0 mm); pleura small and broadly rounded ventrally, none with angular caudoventral angle; pleuron of first segment clearly overlapped by that of second. Telson (Fig. 11*d*) not divided but deeply incised laterally and caudolateral angles of cephalic section bearing two pairs of spines, more mesial pair smaller and movable. Proximal podomere of uropod with mesial lobe bearing acute angle, lateral one rounded; mesial ramus with distolateral spine and smaller premarginal distomedian spine.

Cephalomedian lobe of epistome (Fig. 11*k*) subtriangular with cephalomedian prominence; cephalolateral margins elevated ventrally and only slightly undulant; main body of epistome depressed but lacking fovea. Ventral surface of proximal podomere of antennule lacking spine. Antennal peduncle without spines, flagellum falling short of caudodorsal margin of carapace. Antennal scale (Fig. 11*j*) small, just reaching base of acumen and penultimate podomere of antennular peduncle; lamella broadly rounded distomesially, broadest distal to midlength, but only slightly wider than thickened lateral part. Mandible (Fig. 11*g*) with cornified subtriangular area of caudal molar process proportionately much smaller than that of *F.* (*F.*) *devastator* and farther removed from corneous tuberculiform cephalic molar process. Ventral surface of ischium of third maxilliped with lateral row of short, plumose setae, and mesial half bearing clusters of longer stiff setae; basis with conspicuous cluster of long setae obscuring proximal part of ischium.

Right chela (Fig. 11*o*) about 2.2 times as long as broad, rather strongly depressed; width of palm about 1.7 times length of mesial margin, latter bearing row of seven tubercles and one prominent one lying slightly dorsal to row between third and fourth from proximal end; irregular row of six much smaller tubercles on dorsal flank of mesial row; dorsal surface of palm and fingers bearing setiferous punctations, those on and adjacent to base of fixed finger and on proximal half of dactyl conspicuous; lateral margin of chela rounded proximally, but largely costate; ventral surface punctate except for single prominent tubercle opposite base of dactyl, ventrolateral arc of punctations, each made prominent by long stiff seta, extending from base of palm to base of distal third of fixed finger. Both fingers with well defined submedian ridge flanked by punctations dorsally; ridges on ventral surface less well defined. Opposable margin of fixed finger with row of four tubercles (third from base largest) along proximal third and one projecting from lower level slightly distal to midlength; single row of minute denticles extending from third tubercle from base to corneous tip of finger. Opposable margin of dactyl with obvious excavation proximally, two tubercles borne on margin of excavation and one marking its distal extremity, all subequal in size; single row of

minute denticles extending from distalmost tubercle to corneous tip of finger. Mesial margin of dactyl bearing setiferous punctations, lacking even basal tubercles.

Carpus of cheliped about 1.4 times as long as broad and approximately 1.7 times as long as mesial margin of palm. Dorsal surface with deep submedian longitudinal sulcus flanked by setiferous punctations; mesial surface of podomere tuberculate, that on distal margin acute and much larger than more proximal ones; lateral and ventral surfaces punctate; ventrodistal margin with two acute, corneous tubercles: one on ventrolateral condyle and other mesial to it. Merus with few squamous to rounded tubercles near dorsodistal extremity, two somewhat larger than others; mesial and lateral surfaces finely punctate; ventral surface with mesial row of eight tubercles (nine on left); usual lateral row absent but single tubercle present on left member; lateral row of tubercles characteristic of most crayfishes absent; longitudinal row of long, stiff setae present. Ischium punctate, lacking tubercles ventromesially. Chela of second pereiopod with marginal row of setae on palm, and carpus with dorsal row of long setae; mesial surface of carpus and propodus lacking tufts of plumose setae.

Ischium of third pereiopod only with hook (Fig. 11*m*); latter simple, not overreaching basioischial articulation, and not opposed by tubercle on corresponding basis. Coxa of fourth pereiopod with knoblike caudomesial boss which, if leg extended laterally, projecting mesially. Coxa of fifth pereiopod devoid of boss, ventral membrane setiferous.

First pleopods (Fig. 11*b, f, h*) reaching coxae of third pereiopods and largely hidden by setae extending mesially from ventral margin of sternum. When abdomen flexed, however, apices of terminal elements protruding ventrally beyond setal curtain. Proximomesial spur lacking. Shaft of appendage only slightly bowed, with two terminal elements disposed caudally at about 90 degrees. Mesial process somewhat spatulate, shallowly chamfered, and tilted laterally. Corneous central projection bladelike, with distinct subapical notch, arched and reaching caudally to about same level as mesial process.

Allotypic female.—Differing from holotype in other than secondary sexual characters as follows: acumen not quite reaching base of ultimate podomere of antennular peduncle; postorbital ridges not reaching level of posterior margin of orbit. Abdomen subequal in length to carapace. Distolateral spine on mesial ramus of uropod greatly reduced (perhaps abraded), that on right represented by no more than angle; because of encrustation, dorsal surface of telson and uropods appearing much more strongly setose than that of holotype; both lobes of proximal podomere of uropod rounded. Antennal scale slightly overreaching acumen and base of penultimate podomere of antennular peduncle. Mandible with cephalic molar process strongly abraded, caudal molar process lacking corneous elements. Mesial margin of palm of right chela (Fig. 11*n*) with row of 5 tubercles (left with 6) and row of 4 on dorsal flank (left lacking second row but with single tubercle, between fourth and fifth, ventral to row); dacytl with 2 small tubercles distal to 3 associated with proximal excavation; ischium with ventromesial row of 12 tubercles (11 on left). (See Table 2 for mensural features.)

Annulus ventralis (Fig. 11*i*), 1.5 times as broad as long, situated deeply in sternum; cephalic region immovable, but caudal two-thirds capable of hingelike motion. Sulcus shallow and narrow cephalically, becoming deeper and broader caudosinistrally; high, prominent caudal wall cut by C-shaped sinus arising from fossa at caudosinistral side of sinistrally projecting tongue. Postannular sclerite less than half as long and approximately half as wide as annulus with punctate, oval, ventrally elevated median area.

Morphotypic male, form II.—Differing from holotype in following respects: Tip of

Table 2.—Measurements (mm) of *Fallicambarus* (*F.*) *gilpini*.

	Holotype	Allotype	Morpho-type
Carapace:			
Entire length	22.0	24.9	28.3
Postorbital length	19.1	21.7	25.3
Width	10.1	11.6	13.0
Length	10.0	10.9	12.1
Areola:			
Width	—	—	—
Length	8.9	10.0	11.4
Rostrum:			
Width	3.5	3.5	4.2
Length	3.1	3.7	3.9
Right chela:			
Length, palm mesial margin	3.2	3.3	4.8
Palm width	5.4	6.5	7.4
Length, lateral margin	11.8	12.7	15.2
Dactyl length	8.1	8.5	10.1
Abdomen:			
Width	7.3	7.7	9.3
Length	19.8	25.1	25.0

rostrum abraded but acumen reaching mid-length of penultimate podomere of antennular peduncle. Postorbital ridges terminating slightly posterior to caudal margin of orbit; lateral surface of branchiostegites granular; telson divided; both lobes of proximal podomere of uropod rounded; main body of epistome with cephalomedian fovea; left antennal scale as in allotype, right with regenerated distolateral spine; right chela with only five tubercles in row on dorsal flank of mesialmost row; opposable margin of fingers armed as in allotype; opposable margin of dactyl of left chela with seven tubercles, four associated with excavation and three distal to it.

Except for terminal elements of first pleopod (Fig. 11*c, e*), no noteworthy differences noted between morphotype and holotype. Mesial process more robust with less conspicuous groove, but projecting caudally much beyond tip of central projection; latter, in addition to being stouter and noncorneous, also lacking subapical notch.

Color notes.—Basic color pale greenish blue, but cephalic region more lavender than blue; rostral margins and postorbital ridges distinctly dark green. Mandibular adductor and posterior part of gastric area lavender with faint greenish suffusion. Lateral cephalic region fading to white ventrally, but with paired small navy blue spots midway between tip of rostrum and caudal extremity of cervical groove and another less well defined pair abutting cervical groove. Thoracic area dark greenish blue dorsally, suddenly changing to white laterally, and at least half of branchiostegite white. First abdominal tergum dark greenish blue, second slightly paler, and third through sixth yet more pale with faint hint of very pale dorsomedian longitudinal stripe; white margin of all pleura partly separated from blue to bluish green tergum by series of short dark greenish blue bars. Telson with cephalic section mostly bluish, caudal section colorless and translucent; lateral section of lateral ramus of uropod pale bluish green, keels of both rami and margins of basal podomere dark greenish blue. Antennules and antennae with lateral and mesial borders of peduncles darker blue than dorsal and ventral surfaces; flagella greenish blue basally fading to pale tan. Cheliped with dorsal surface of distal part of merus, carpus and chela dark bluish green; tips of fingers yellowish with corneous brown tip; ventrolateral part of palm and fixed finger fading to cream; ridges and tubercles on carpus and palm of chela very dark blue. Venter and basal podomeres of remaining pereiopods white; dorsum of merus, carpus, and propodus of second through fifth pereiopods bluish green, dactyl with some blue but more cream to yellowish.

Size.—The largest specimen available is a second form male having a carapace length of 28.8 (postorbital carapace length, 26.0) mm. Corresponding measurements of the smallest first form male were 21.1 and 18.8

mm, and those of the smallest ovigerous female, the allotype, are 24.9 and 21.7 mm, respectively.

Type locality.—Roadside seepage 3.1 mi south of southern junction of State Route 54 and U.S. Highway 79 at junction of latter with Pepperridge Road (T7S, R10W, Sec 19), approximately 11 miles south of Pine Bluff and about 3 miles north of Cleveland County line, Jefferson County, Arkansas.

Disposition of types.—The holotype, allotype, and morphotype (USNM 219511, 219512, and 218944, respectively) are deposited in the National Museum of Natural History, Smithsonian Institution, as are the paratypes consisting of 1 ♂ I, 1 ♂ II, 8 ♀, 2 juv ♂, 2 juv ♀, 2 ovigerous ♀.

Range and specimens examined.—All of the specimens were collected from burrows in roadside seepages in Jefferson County, Arkansas: (1) type locality, 1 ♂ II, 26 Apr 1986, HWR; 5 ♀, 2 juv ♂, 2 juv ♀, 18 Mar 1987, HWR (two additional juvenile males were maintained in aquaria until they molted to first form, one in late Feb 1988, and the other, the holotype, on 9 or 10 Apr 1988). (2) 0.2 mi S of Pine Bluff city limits, 1 ♀, 11 Apr 1986, HWR, coll. (3) 3.6 mi N of Cleveland Co. line on US Hwy 79, 2 ♀, 7 Nov 1987, B. F. Kensley, HWR, HHH; 2 ♂ II, 2 ♀, 3 ovig ♀, 11 Mar 1988, HWR.

Variations.—Among the adult specimens, the areola constitutes from 38.1 to 40.6 percent of the total length of the carapace, and from 42.1 to 46.6 percent of the postorbital carapace length. Most of the differences noted in the specimens may be attributed to abrasion and to regeneration of chelipeds. The former is reflected in the absence of an upturned tip on the rostrum, reduced and/or truncated tubercles and spines, and broken or missing setae (particularly noticeable on the third maxillipeds of specimens in late intermolt stages). Regenerated chelipeds can usually be recognized by the absence or reduction of the excavation on the proximal part of opposable margin of the dactyl of the chela, but also by the smaller, and frequent increase in number of tubercles on the opposable margins of both fingers. The number of tubercles in the ventromesial row on the merus of the cheliped ranges from 7 to 11, on the mesial margin of the palm of the chela, from 5 to 7 with 0–6 on the dorsal flank; on the opposable margin of both fingers, there are from 4 to 6 tubercles (in one specimen 2, instead of 1, lie at a lower level on the fixed finger). There is no noteworthy variation in the secondary sexual features of the two available first form males, and in the female, the only conspicuous difference observed is the anticipated occurrence of a mirrored image of features of the annulus described in the allotype.

Life history notes.—No first form male has been collected, and the only two available were reared from very small juveniles collected in March 1987. They were maintained in the laboratory in Washington, D.C., and molted to first form in late February and early April 1988. Three ovigerous females were dug from burrows on 11 March 1988: one with carapace length of 22.3 mm carried 18 eggs along with several empty "capsules," another with cl of 24.9 mm, 20 eggs, and the third with cl of 25.5 mm, 35 eggs. All of the eggs were about 2 mm in diameter. The two juvenile females collected on 18 March 1987 have carapace lengths of 11.9 and 12.1 mm, and the two juvenile males, 11.4 and 11.9 mm.

Ecological notes.—This crayfish has been found only in complex burrows consisting of branching galleries, several of which, except in dry seasons, reach the surface, some of their openings marked by rather crudely constructed turrets. Where *Fallicambarus* (*C.*) *gilpini* has been collected in the same locality with *F.* (*C.*) *fodiens,* the burrows of the former were frequently, if not usually, situated higher on the seepage slope, suggesting that like the partitioning of a habitat in South Carolina by *Cambarus* (*J.*) *carolinus* (Erichson, 1846) and *Distocambarus* (*Fitzcambarus*) *carlsoni* Hobbs, 1983 (see

latter, page 437), *gilpini* might prefer areas in which the groundwater is moving, whereas *fodiens* more frequently occurs in areas in which the water is more static. In general, the burrows of *gilpini* are more complex, exhibiting more subhorizontal galleries than do those of *fodiens* that we have excavated in Arkansas.

Relationships.—*Fallicambarus* (*C.*) *gilpini* has its closest affinities with *F.* (*C.*) *caesius*. In addition to the many features the two species share in common, including being the only typically blue members of the genus, they are the only ones that lack a ventrolateral row of tubercles on the merus of the first cheliped. The most readily observed features that distinguish the two species are the absence of tubercles on the mesial surface of the dactyl of the chela and the presence of a distolateral spine on the mesial ramus of the uropod in *F.* (*C.*) *gilpini*.

Etymology.—This crayfish is named in honor of our mutual friend Robert H. Gilpin, of Cumberland, Maryland, in token of his interest and assistance in collecting much of the material we have from the eastern part of Arkansas.

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